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OUTLINES

OF

GENERAL ZOÖLOGY

BY

HORATIO HACKETT NEWMAN

PROFESSOR OF ZOÖLOGY
IN THE UNIVERSITY OF CHICAGO

Third Edition

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PREFACE TO THE THIRD EDITION

One of the most striking trends in college education during the last decade is that toward orientation, survey, or general courses. In some of the larger institutions the backbone of the program of general education in the first two years consists of a series of general courses covering the various fields of knowledge. In these general courses attempts are made to interrelate and integrate the subject matters of the different branches of science and to discover the broad, general principles that run through the whole.

This trend toward more general types of courses has had a pronounced effect upon the more special types of departmental courses and threatens their very existence. Among the types of more or less isolated special courses that have felt the impact of the oncoming general courses is the traditional type of first year course in zoölogy. In the past most of us have taught our zoölogy as though it were an isolated subject, without any particular relations to other fields of knowledge. It seems certain that we can no longer do this without endangering the survival of general zoölogy courses as such. It is necessary to recognize the existence of the survey courses and their inevitable success. Our best chance to keep the departmental zoölogy courses alive and up-to-date seems to lie in adjusting them to the modern trend by recognizing that our subject has intimate relations with the whole field of knowledge and by fitting zoölogy into its proper place in this field.

The writer has had, perhaps, a unique experience in connection with general courses. Over ten years ago he organized and directed a freshman survey course, *The Nature of the World and of Man.* This course died in giving birth to the four main general courses that form an important part of the so-called New Plan at the University of Chicago. A valuable feature of this early survey course was that some of the teachers in the course admitted that they had become reëducated. The range of their knowledge was increased and they came to see more clearly than formerly the interrelations of the various sciences. Four additional years of intimate association with the present New Plan general course in biological sciences have served still further to change the writer's

perspective and to convince him that general courses have come to stay.

The basic educational purpose of the general courses in the College is that of furthering the broad general education of the student before he enters upon his selected field of specialization. In presenting such courses cultural values are uppermost, but preparation for more advanced courses is not ignored. It seems not unfair to say that some of our first courses in zoölogy have contained too little of that type of material that has definite cultural value and too much of that which is technical from the outset and important only for students who intend to specialize in biology or medicine, a minority group. It would seem advisable then to take care of the needs of the majority without ignoring those of the minority.

This book in its present form is an expression of a definite attempt to meet the new situation by presenting the subject of zoölogy in such a way as to subserve the needs of general education. Our purpose is to meet the survey courses half way, to adapt the zoölogy course to an inevitable trend toward a greater generality of outlook in science courses. In Junior Colleges and other institutions where it is not feasible to introduce the more extensive interdepartmental type of survey course it may well be that such a course as is outlined in this volume will serve as a satisfactory substitute.

The plan of the book involves the introduction of a basic philosophy which combines several interrelated concepts: the organismal view, the theory of progressive levels of life units, and that of emergent evolution. Significant interrelations between biology, astronomy, geology, physics, and chemistry are emphasized. Life units are put in their cosmic setting. The whole story of biology is told in the form of topics that cover the unique properties of living units. The more general principles are presented first, then an adequate series of types is introduced, after which the more complex mechanisms and processes of living units are discussed in a logical and progressive sequence, culminating in the master principle, organic evolution.

In this book the various types are presented in their phylogenetic order beginning with the Protozoa and ending with vertebrates. It is, however, a simple matter for those who prefer to begin with vertebrates to take all of Part IV out of its present position and

put it in advance of Part III. The new introduction to Part IV favors such a change of order.

An effort has been made throughout the book from beginning to end to make the treatment logical and sequential. A unifying thread of principles runs through the whole book, linking topic with topic. The pedagogical scheme of judicious repetition of the same facts or ideas in different connections has been rather extensively employed and needs no apology.

A new feature of the book, and one that is a novel departure in this field, is the summary at the end of chapters where such a summary is feasible. It is difficult to prepare a useful and adequate summary that adds something to real value. In these summaries we have attempted to place emphasis upon the more important facts and concepts, to link up the subject matter of one chapter with that of others, to introduce new generalizations here and there, and to furnish convenient material for review.

In this revision the writer has had the advantage of valuable advice, suggestion, and criticism from his colleagues, especially from Professors W. C. Allee and A. E. Emerson, to whom he is duly grateful. Needless to say, much of the book has been completely rewritten, but a great deal of it remains unchanged or modified only sufficiently to conform with the new plan and to comply with the expressed needs of teachers who have used the book. It is hoped that friends of the earlier editions will find the new one a distinct improvement.

For teachers who desire a laboratory manual especially designed to accompany this text in its present form, Mrs. Katherine McClure Roehl and the writer have prepared one that has been thoroughly tried and modified in the light of experience.

H. H. Newman

The University of Chicago
May, 1936

PREFACE TO THE FIRST EDITION

During more than a score of years the writer has had an exceptional opportunity of studying the changing styles of teaching employed in courses in General Zoölogy in representative American universities and colleges. In the earlier days it was the fashion to use the *type method* exclusively, conducting the student through a cursory survey of the animal kingdom with the idea of affording him at least a speaking acquaintance with as many as possible of the representative animal types. The superficiality of this method became increasingly apparent as time went on, and the natural remedy was to abbreviate the list of types studied and to concentrate on a few of the most important forms, these selected so as to represent the various levels of organic complexity. The idea underlying this departure—an idea not without justification—was, that a few animals intensively studied illustrate the essential principles of the subject as well as or better than a much larger number studied superficially. Intensive work, moreover, tends to inculcate ideas of exactitude in observation and skill in laboratory technique.

Out of the type-study method there gradually evolved another method—that of the study of principles. At first, the principles were merely brought in as side issues to lend interest to types. Gradually, however, the principles came to assume larger and larger proportions until they overshadowed types altogether. Thus evolved the *principles method*. According to this method types, as such, were abandoned, and the subject matter of zoölogy at least as much of it as admitted of such treatment, was presented as a series of principles. Animal forms were mentioned only incidentally as illustrative materials, no one animal being studied at all completely. This method had a measure of success in some institutions, but the common experience has been that the student can go just so far in a study of principles before he begins to feel an insistent demand for a more concrete knowledge of animals themselves. He asks: "What is this Amœba, this Hydra, this Planaria?" The instructor is then forced to stop and introduce

some of these real animal types before he can profitably go ahead with his teaching of principles.

The experience of the writer and of his colleagues has, we understand, not a few points in common with that of the majority of teachers who have tried the principles method. We have been forced to revert to some of the tried and proven features of the type method, while retaining what seem to us the best features of the principles method. Thus we have adopted a workable compromise between the old and the new methods; and the present text is an embodiment of our experience as to the content and arrangement of materials for a well-rounded course in General Zoölogy.

Our method is, in general, as follows: We begin with a historical survey; we follow this up with a general discussion of the problems associated with life, protoplasm, and the cell; it then becomes necessary to present a series of animal types, ranging from Amœba to the frog, each type being used as a concrete illustration of one or more principles; finally, a return is made to matters of general biology, the topics leading logically up to the principle of organic evolution.

If the instructor prefers to introduce the vertebrates first, he may, without any other adjustment of materials, take out bodily the section on the frog and transfer it to a position in advance of that on the Amœba, and then proceed through the other topics in the order given. There may be too much material in the book for a major or a semester course as offered in some institutions. In that case various chapters, according to the judgment of the instructor, may be omitted without impairing the unity of treatment. There is, on the other hand, sufficient material for courses given throughout the year; and this certainly would be the case if some of the shorter chapters were to be expanded by the instructor.

It need hardly be said that the author has drawn upon a great variety of sources for the data presented in the book. In some cases the materials of other authors have been incorporated with little change in thought or point of view and with only sufficient modification in language or in order of presentation to make it fit into the place assigned to it. In general, it is hoped that old facts have been presented with at least an added touch of newness either of expression or of point of view.

The author has tried to avoid the error of overillustration not uncommon in textbooks of the present day. No figures are used except where an illustration seems necessary to supplement the material given in the text. In this place the author would like once more to acknowledge his indebtedness to Mr. Kenji Toda, whose skill with the pen has done much to lend freshness to the book.

For constructive criticism the author is indebted to his colleagues, Professors W. C. Allee and A. W. Bellamy, who read considerable parts of the manuscript, and to the skilled reader employed by the publishers.

Most of the illustrations used in the book, other than those drawn or redrawn, have been borrowed from The Macmillan Company's publications; and acknowledgments are due to the following authors: T. J. Parker and W. J. Haswell, E. B. Wilson, R. W. Hegner, S. W. Holmes, Ulric Dahlgren and W. A. Kepner, R. S. Lull, L. L. Woodruff, H. E. Walter, W. B. Scott, A. E. Shipley and E. W. MacBride. Some of the most valuable illustrations have been borrowed, with permission, from books published by other companies, and we herewith express our indebtedness to both authors and publishers of the following books: *Evolution and Animal Life*, by D. S. Jordan and V. L. Kellogg (D. Appleton & Co.); *Genetics in Relation to Agriculture*, by E. B. Babcock and R. L. Clausen (McGraw-Hill Book Co.); *Principles of Animal Biology*, by A. F. Shull *et al.* (McGraw-Hill Book Co.); *Biology*, by G. N. Calkins (Henry Holt & Co.); *General Biology*, by W. T. Sedgwick and E. B. Wilson (Henry Holt & Co.); *Zoölogy*, by T. D. A. Cockerell (World Book Co.); *Biology, General and Medical*, by J. McFarland (W. B. Saunders Co.); *Individuality in Organisms*, by C. M. Child (University of Chicago Press); *Animal Communities in Temperate America*, by V. E. Shelford (University of Chicago Press); *The Biology of Twins*, by H. H. Newman (University of Chicago Press). Finally, a considerable number of illustrations and much valuable data have been obtained from books, monographs, and shorter articles published either in journals or privately. While a complete list of these cannot well be given here, the author would like to acknowledge his indebtedness to the following: C. O. Whitman, E. B. Wilson, E. G. Conklin, T. H. Morgan, F. R. Lillie, C. M. Child, W. E. Ritter, J. A. Thomson, A. Dendy, A. E. Shipley, E. W. MacBride, H. S. Jennings,

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The writer is not unmindful that some controversial matters have been handled in more or less partisan fashion, but he feels that the purely neutral position is a deadly one for a teacher to take. If the instructor feels called upon to take an opposed view as to any or all of the points at issue, he will at least have a good opportunity of starting a class discussion; and discussion is the very life of class work.

H. H. Newman

The University of Chicago
June, 1924

PREFACE TO THE REVISED EDITION

In the five years that have elapsed since this book was issued, teachers have had a sufficient opportunity to discover its stronger as well as its weaker points. The outstanding feature of the book was its judicious blending of the principles method and the type method of presenting the materials of General Zoölogy. This feature has stood the test of time and needs no modifications in principle. Several teachers, however, have asked for the introduction of more types and have specified those most desired by them. Others have requested more material about some of the types already in use, notably the earthworm and the frog.

In general, it now appears that the main criticism of the first edition was that it did not contain quite enough material for a two-semester course. Closely following the needs that seem to be most commonly felt by teachers, the writer has introduced several new types: the sponges, the clam, parasitic roundworms of man, and the grasshopper. Rather extensive additions have been made to the chapters on the earthworm and the frog.

Prompted by the splendid new edition of *The Cell*, by E. B. Wilson, the chapter on the Morphology and Physiology of the Cell has been completely rewritten. The chapter on The Animal Kingdom has been materially enlarged by the addition of a discussion of the interrelations of the animal phyla along the lines of the new *Diphyletic Tree Theory*. This idea seems to add unity and coherence to the whole section of the book dealing with animal types.

The most important improvement in the book involves the materials presented in Part IV, which was formerly entitled General Principles of Zoölogy. Competent critics suggested that this part of the book, while it contained materials indispensable for a beginning course, was loosely organized and lacked sequence and coherence. This section of the book has now been rearranged and extensively rewritten under the general title of Dynamic Aspects of Zoölogy. It was found that nearly all of the materials formerly treated as principles could readily be dealt with as biological mechanisms for regulating the interactions of

the parts of the organism, for adapting the organism to the environment, and for racial change and adjustment. A few old sections seemed not to fit into this scheme and were omitted, while three new chapters on BIOLOGICAL MECHANISMS, COÖRDINATING AND REGULATING MECHANISMS, and SENSE ORGANS have been added. A criticism of the first edition was that it did not give enough material on physiology. It will now be seen that the new Part IV carries a physiological tone throughout.

In its present form this text is now believed to be as well adapted for courses lasting a whole college year as for those confined to one semester or one quarter. For those covering the subject in a briefer way it is suggested that a good many of the chapters on types be omitted and that Part IV be dealt with only in brief outline. Selections and omissions will, of course, depend upon the individuality of the teacher.

In revising this text the writer has had the advantage of kindly criticisms of several of his colleagues, especially Professors W. C. Allee and B. H. Willier and Dr. L. H. Hyman, for which he is duly grateful.

The book in its present form is a tangible expression of the writer's appreciation of the many kindly suggestions and constructive criticisms on the part of the users of the first edition. Everything has been done to comply with requests and suggestions in so far as these have been compatible with the general purpose, plan, and scope of the book. The publication of a *Laboratory Guide and Review Manual* to be used especially with this text constitutes a response to one of the most oft-repeated requests on the part of teachers using the first edition.

H. H. NEWMAN

THE UNIVERSITY OF CHICAGO
March, 1929

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PART I

BIOLOGICAL SCIENCE AND ITS HISTORY

CHAPTER I

THE SCIENCE OF BIOLOGY

A. Definitions

Zoölogy is that branch of natural science devoted to the study of animals. A synonym for Zoölogy is animal biology. We prefer the term Zoölogy because that is the usual name applied to university departments dealing with the biology of animals and because courses in such departments are usually listed as Zoölogy courses. Zoölogy is, moreover, as appropriate a name for animal biology as is Botany for plant biology.

Botany and Zoölogy together constitute the science of biology. The term biology was invented early in the nineteenth century by Lamarck and by Treviranus independently of each other and was soon adopted by all writers on the subject. The word biology is derived from two Greek words, *bios* (meaning life) and *logos* (meaning literally discourse, but now freely translated as study or science). We may therefore define biology as the science of living things or the science of life.

B. The Complexity of Zoölogy

At the risk of seeming to glorify our own particular science, it may be said, with the assurance that few will disagree, that Zoölogy is one of the most intricate of all the sciences. It may be thought of as a sort of superstructure built upon the solid foundations reared by the physical sciences (Physics, Chemistry, Geology). Its framework is Philosophy; the sciences of Mathematics and Engineering furnish the tools and the instruments of precision. Training for advanced work in Zoölogy involves a preliminary training in all of the sciences mentioned, and frequently more. Ofttimes the zoölogist has had to turn inventor in order to equip himself with the necessary instruments with which to carry on his researches. Thus biologists have had much to do with the gradual improvement of the compound microscope and with microphotography. Many temperature regulating and temperature registering instruments of great delicacy have been the self-made

tools of biological explorers. Many a beautiful piece of apparatus designed by biologists for their own uses has been found to have a much wider application.

The rather widespread impression that Zoölogy is merely a study of "bugs" and that zoölogists are "bug-hunters," is gradually giving way before a growing conviction that Zoölogy is a serious and valuable subject. Its problems are the most complex and difficult of solution among the problems of science, and they require the best efforts of the best intellects for their successful solution. Zoölogy is a science of unsolved or only partially solved problems, many of them baffling in their elusiveness and intangibility. Some of our very earliest and most pressing problems are still unsolved, and progress in many other lines is retarded by our failure to solve them. Such an unsolved problem is the perennial mystery: what is life? Until we can answer this, the ultimate solution of many another knotty problem will be held in abeyance. A list of some of the larger problems and principles and theories that constitute the framework of the science of Zoölogy will perhaps make plain to the uninitiated reader something of the nature and content of zoölogical science.

C. Some of the Problems That Face the Biologist

1. When, where, and how did life first begin?
2. Does new life ever arise today except as the progeny of living things? The problem of Abiogenesis.
3. What is life? The problem of the nature of life.
4. What is the physical basis of life? The protoplasm problem.
5. Is death of the individual inevitable? The problem of the nature of death.
6. Can life be explained as an expression of matter and energy changes in complex units, or does it involve something besides matter and energy? Mechanism versus Vitalism.
7. Are the properties of an organism fully to be explained as a summation of the properties of its parts, or are there properties of the whole that transcend those of the parts? The organismal versus the elemental points of view.
8. What are the factors that integrate the parts of an organism and make the latter an individual?
9. What is the mechanism of mechanical movement in living units? The problem of pseudopodial, ciliary, and muscular movement.
10. What is the mechanism of behavior in the simpler organisms? Tropism and trial-and-error theories.
11. What is the true function of sex in organisms?

12. How is sex determined?
13. What is the significance of fundamental resemblances between different groups of organisms? The Principle of Homology.
14. To what extent are the characters of the individual predetermined in the germ cell and to what extent are they the result of developmental processes? The problems of Preformation and Epigenesis.
15. How do new characters arise in a species?
16. What are the factors responsible for the fitness of the organism to the environment? The adaptation problem.
17. How much of fitness is the result of individual modification or adjustment?
18. How much of adaptation is purely hereditary?
19. What are the factors governing the geographic distribution of different kinds of animals?
20. Why is there so much popular opposition to the idea of organic evolution?
21. Has the general principle of evolution been proved to be a fact? If so, what is the nature of such proof?
22. In exactly what ways do the so-called evidences of evolution afford proof of the validity of that principle?
23. What are the factors involved in the origin of species? The speciation problem.
24. What are the chief causal factors of progressive evolution?
25. Are the acquired bodily improvements of parents, due to training, etc., passed on to offspring? The problem of the inheritance of acquired characters.
26. To what extent does Darwin's theory of "the survival of the fittest" explain progressive evolution?
27. What can be said as to the relative potency of differences in heredity and in environment in determining the characteristics of an individual?
28. What is the nature of the mechanisms of hereditary transmission?
29. What is the nature of nervous activity? Of the nervous impulse?
30. What is meant by intelligence?
31. What is the nature of instinct?
32. What is known about the ancestry of man?
33. What is the probable future of man on the earth?

These are only a few of the problems that confront the student of Zoölogy. Only such problems have been placed in this list as may have been at least casually encountered by thoughtful students by the time they have reached the college level. Many additional problems will be raised and discussed in the body of the text. For the present it should suffice if the beginning student receives the impression that biology is, like other sciences, full of problems. Hardly one of the problems listed above can be said to be fully solved; only a few of them are as much as half solved;

many of them are still entirely unsolved. Many special or minor problems that are corollaries of or accessory to the major problems mentioned have been studied intensively and may be considered, at least tentatively, as solved. Many both major and minor problems, doubtless capable of solution, have as yet never been adequately explored. The field of Zoölogy then is untilled ground. We zoölogists are just beginning to catch glimpses of what the future has in store for us. Zoölogy is a splendid field for young and able investigators, for there is no dearth of problems worthy of their best endeavors. Every new discovery throws light on several other points and thus paves the way for further discoveries. All of the problems are so interrelated that they require for their solution a massed attack on some few of the major problems and minor attacks from various angles on the secondary strategic points.

This outlook upon Zoölogy as a body of insistent problems demanding solution is beyond question most stimulating both to novices and to veterans. It lends life and interest to the discussion of the numerous phenomena that make up the factual basis of the subject. The student must learn to view knowledge as to a large extent tentative, subject to correction, and ready for complete revision in the light of new discoveries. This is the spirit of modern science, and this should be the spirit of each student of Zoölogy.

D. The Nature of the Materials of Biological Science and the Methods of Studying Them

The Nature of Science.—Any science is a body of facts, principles, hypotheses, theories, and laws about some limited field of natural objects. Facts are the indispensable building stones of science. Facts are the fruit of carefully repeated and rigidly checked observations and are only accepted when, after repeated observation by numerous observers, there is general agreement about them. Real facts represent truth and the scientist is one who respects truth above opinions or beliefs, no matter how time-honored the latter may be. Science is founded on accurate observation of facts and relies on the validity of the senses as revealers of the truth about objects. Of course the senses may sometimes deceive us, but crude sensory perceptions may be aided and checked by instruments of precision, by experimental manipulation and by the use of mathematics. The observations made by this

method must be accepted as representing the world of reality that science deals with. It is legitimate enough to question the ultimate reality of the world revealed to us by the aided and unaided senses, but this questioning of the reality of the materials of science is the province of philosophy and therefore beyond the scope of science itself.

The Methods of Science.—It has often been said that "the essence of science is its method." What science tries to do is to explain the phenomena of nature in terms of the causes or mechanisms involved in the observed objects or processes. It is realized that few if any objects or processes are the result of any single cause: on the contrary, it has been discovered by hard experience that even in the simplest case several or many causes interact to produce an observed result. We therefore speak not so much of single causes as of FACTORS, whose interactions bring about the result. One of the commonest errors committed by workers in all fields of science is that of attributing a given observed condition to one cause and of failing to recognize that other factors may also be involved. Only by careful and thorough experimentation is it possible to discover and isolate the factors involved in a biological process. The mere discovery that condition A is always present when event X occurs is not sufficient to prove that A is the only factor involved. Yet many conclusions have been based on such reasoning. The more we learn about biology the more we become convinced that even the simplest of biological processes are very complex and that we should be skeptical about all theories that explain such processes too simply.

What we have just said has to do with the methods of determining facts and analyzing them in terms of the factors involved. In so doing we discover *immediate* causal relationships between factors and events, but we do not discover *ultimate* causes. Ultimate causes are beyond the field of science. This process of experimentally analyzing biological events into the system of factors involved is the ideal method when such a method is practicable, but there are vast fields of biology that because of their very nature cannot be submitted to experimental analysis. Obviously, the experimental-analytical method is limited to existing phenomena and cannot be applied to a study of past conditions or events. When one tries to reconstruct the events of the remote past he must use the HISTORICAL METHOD, that of seeking records of the

past in whatever forms they are found and attempting to reconstruct the history of the past. A good example of a field that requires the historical method of approach is that of ORGANIC EVOLUTION, the long-time process of change through which organisms of today have passed since the origin of life on the earth. We cannot experiment with the past: that is obvious. But we can experiment with the present to determine first, whether evolution is still going on and what are some of the basic factors involved. Then, relying on the principle that life today is a continuation of life in the past and that much the same processes that have gone on in the past are still going on today, we can assume that what we find going on today is the same sort of thing that took place in the past. This is not perfectly safe reasoning, but is the type of reasoning used by nearly all modern students of evolution and no better mode of reasoning has been suggested. There are ways of checking this conclusion. We can examine the living things of today to see whether or not they show evidences of having evolved along lines suggested by the analysis of processes of change going on today. We can examine the animals and plants of the past (fossils) to see whether they have changed from age to age in ways that accord with the mechanisms known to be operating today. Then we can examine all sorts of new facts and relations to see whether these are in accord with or are opposed to our theory that the processes going on in the present have also operated in the past. If we find that all the evidence favors this conclusion and none contradicts it, we consider this conclusion a well-tested theory or an established principle—even a law. For a LAW OF NATURE is no more than a statement about a process that holds good for all known cases.

By means of experimental analysis and by means of the historical mode of reasoning and evidence gathering described in the last paragraph, we have accumulated a large body of principles, theories, and laws—great generalizations that form the foundations and the principal framework of biological science. Around these major principles are clustered many minor principles, hypotheses, theories, and laws. Biologists realize that the theories of today are far from being final explanations: they are merely the best explanations we can give at the present time in the light of the facts and evidences now available. A biologist never is, or at least should not be, dogmatic even about the best established prin-

ciples of his subject. He is, or should be, ready to modify his theories whenever new knowledge compels such modification.

E. The Values of Zoölogy

The human values of the study of Zoölogy are mainly two: cultural and practical. In this book we are more concerned with the former than with the latter. It is surely an important part of a general education of every student to understand to some extent the living world of which he is a part. A knowledge of the rest of the living world gives him a better understanding of himself. The highest cultural values of biological study result from the fact that it widens the intellectual as well as the æsthetic horizons of those who pursue it. Some of the major biological concepts such as that of orderly change in the universe, the immense time consumed in the process, the progressive branching out of groups into a multiplicity of diverse types each adapted to play its own peculiar rôle in nature, the intimate interdependencies of these varied types of living things, the balance of nature, the unity combined with variety in living things, the wonderful constancy and regularity of some vital mechanisms: these and many other concepts tend to increase our admiration and respect for the world of life and change our perspective with regard to ourselves. Far from taking the beauty out of life, the study of biology enhances and vivifies it, adding many new and unsuspected vistas more beautiful than those naïvely perceived by the untrained observer. It has been truly said that the proper study of biology has "an æsthetic value entirely comparable with the finest in art and poetry."

The **practical values** of the study of biology, especially of zoölogy, are more or less obvious. Zoölogy is one of the prerequisites for the study of medicine. Most of the great discoveries as to the nature and control of disease have been obtained through animal experimentation based on the knowledge that the physiological processes in animals and man are basically the same. What is discovered to be true for the dog, the guinea pig, the rabbit, and the rat, our common laboratory animals, usually applies to man. It is believed that at least the preliminary experiments upon the problems of health and disease are much more properly carried out upon dogs, guinea pigs, and rats than upon human subjects. Strange as it may seem, biologists are constantly forced to defend their right to use animals for scientific investigation. Antivivisectionists, posing as animal

lovers, endeavor to have laws enacted prohibiting the use of live animals for experimentation. If such laws were to be passed and enforced, progress in medical and biological science would be greatly impeded, with a proportionate increase in human suffering. Need we say more?

Agriculture.—Zoölogy is also of great importance in agriculture. Vast wealth in crops is destroyed annually by injurious insects and only a knowledge of the biology of these insects enables us to combat their attacks. It is said that the crop loss due to insects amounts to a value of over half a billion dollars annually and that most of this loss could be prevented were our knowledge of the methods of insect control put into practice. Losses almost as amazing are caused every year by the attacks of diseases and parasites of our common domestic animals (cattle, hogs, sheep, poultry, etc.) through the attacks of bacteria, parasitic protozoans, worms, and insects. Knowledge of the biology of these parasites and its proper application would save untold millions of our living wealth.

Fisheries.—One of the most important practical applications of zoölogy is in connection with fisheries. The government maintains a Department of Fisheries, with scores of stations, for the study of fish culture. Knowledge has been gained that has prevented the extinction of many of our most important food fishes, such as salmon, whitefish, and herring, to mention only a few. Within the scope of the Department of Fisheries come also the culture and propagation of such important food animals as lobsters, shrimps, oysters, and other important food animals, as well as inedible forms such as commercial sponges.

Forestry.—Another branch of applied biology that makes use of a scientific knowledge of animals is Forestry. Many of the chief enemies of trees are insects that sometimes reach such numbers as almost to exterminate over extensive regions such important timber trees as pines and hemlocks. A knowledge of the life cycles of these pernicious insects, their natural enemies and methods of preventing their spread, has gone far to save our most important timber resources.

Eugenics.—Slowly but surely we are accumulating a knowledge of the facts of variation, heredity, and other factors in human evolution. This knowledge has been made possible through studies of the modes of evolution of animals suitable for experimental breeding, notably the humble fruit fly, Drosophila. Such knowledge,

when fully checked and confirmed, can be used in directing the course of human evolution. The practical application of the laws of variation and heredity to the betterment of human stocks is the province of Eugenics. While some ardent eugenists urge the immediate adoption and practice of rather drastic eugenic measures, the more conservative students of human genetics feel that now is the time for more intensive investigation of the facts of human heredity. When the facts are thoroughly understood it will be in order to attempt to guide the course of human evolution along paths that will positively improve the race.

F. Subdivisions of Biological Science

Back in the early days of biological science all sorts of facts and fancies about animals and plants came under the general head of NATURAL HISTORY. Two hundred, or perhaps even one hundred years ago, it would have been possible for an able scholar to survey and understand all the then recorded facts of living nature. Such a scholar was called a naturalist. With the steady and rapid accumulation of knowledge about organisms, especially during the last century, it has become impossible for a single man or even a few men to compass the whole field. Consequently there have arisen specialists in numerous subdivisions of the subject and these have confined their researches to more or less narrow regions within the broad field. The earliest subdivision of the field was on the basis of the obvious groupings of natural objects. Thus the biology of plants was called BOTANY and that of animals ZOÖLOGY. Within each of these there are many fields of specialization. Another broad classification of the whole field that does not follow the natural subdivisions of types of organisms but emphasizes perhaps more fundamental aspects of life, is the division into MORPHOLOGY (the study of form and structure) and PHYSIOLOGY (the study of function). A third classification of the whole field may be made on the basis of whether organisms are living or extinct. The study of extinct organisms is called PALÆONTOLOGY, in contrast with the study of living organisms. A fourth subdivision of materials within the whole field is into NORMAL and PATHOLOGICAL. Again, some specialists may concern themselves with the anatomy and physiology of adults and others primarily with a study of the development of the individual. The former are *anatomists* and *physiologists*, the latter *embryologists*. Some specialists are interested primarily

in the structure and functions of whole organisms, others of systems and organs, while still others are interested in the microscopic aspects of the finer parts of organisms. Those interested in the activities of whole organisms in relation to their physical environment or to one another are students of ECOLOGY; those interested in comparing of systems and organs are students of COMPARATIVE ANATOMY and COMPARATIVE PHYSIOLOGY; those interested in the

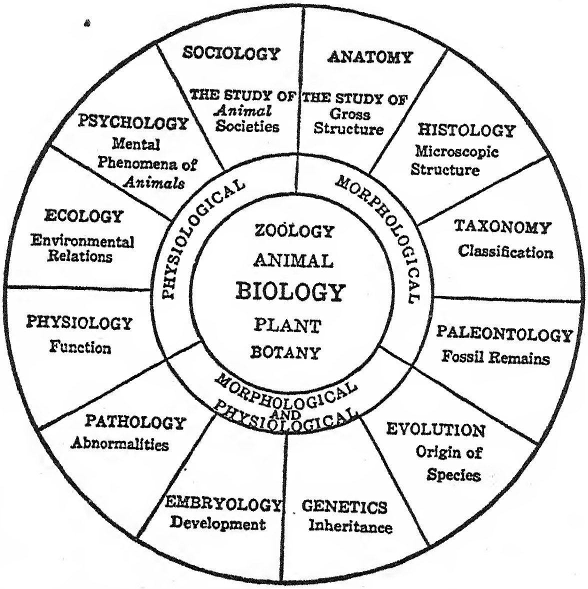

FIG. 1. A diagram showing the interrelations of the chief divisions of biology. From Woodruff.

structure and function of tissues are students of HISTOLOGY; and those dealing with cells are students of CYTOLOGY.

Experience has shown that no single aspect of biological study affords an adequate knowledge of any problem unless other aspects are also considered. Thus it is impossible to understand the physiology of an organ without a knowledge of its tissues and the character of the individual cells involved. It is also difficult to interpret any type of modern organism without a knowledge of its extinct predecessors. Finally, it is futile to try to understand an individual animal without a knowledge of the organic and inorganic environment in which it lives. Thus there is an integrating matrix

that binds all the biological sciences into a coherent system. Such a system is well represented by the diagram (Fig. 1). What has been said suggests that although specialization is essential for progress in science, a firm foundation in general principles and a fairly comprehensive outlook over the whole field is a prerequisite for entering successfully upon any branch of intensive specialization. It is the purpose of such courses as this to lay an adequate foundation for more specialized work in biology as well as to give the person who never expects to be a professional biologist a general grasp of the subject.

SUMMARY

1. Zoölogy is the science of animal life.
2. Science is organized knowledge, involving facts, generalizations, principles, and explanatory theories.
3. The favored method of science is that of analyzing a process into its component factors by means of controlled experiment.
4. Only immediate causes, not ultimate causes, are discoverable by the scientific method.
5. The historical method is useful in attempting to reconstruct events of the past, such as the past evolution of organisms.
6. Zoölogy is full of unsolved problems, and is a fertile field for research.
7. The human values of the study of Zoölogy are first cultural and second practical.
8. Zoölogy today consists of a score or more of different branches of specialization. Only through intensive specialization can real advance in knowledge be made.

CHAPTER II

HISTORY OF ZOÖLOGY

BEFORE entering upon a systematic study of various problems of Zoölogy or of the various types of animals, it is well for the student to take a brief historical survey of the history of the science we are dealing with, to learn how and when and at whose hands the great problems arose, and in how far they have been solved. All history is one: no longer can the church historian understand his subject without a knowledge of political, educational, and scientific history. Similarly, we find that the history of Zoölogy—and particularly the philosophical aspects of it, such as the Principle of Evolution—has been inextricably bound up with religious and secular history. During times of peace and prosperity, when thinkers had leisure to think and were unhampered by artificial religious restrictions, science made great strides. During and after wars, in periods of severe religious dominance and intolerance, in periods of social laxity and overindulgence, science was prostrated and made little progress. The history of Zoölogy has been characterized by long periods of stagnancy and depression. These ups and downs are now to be brought to our attention.

A. THE BEGINNINGS OF ZOÖLOGY

The earliest writers on zoölogical subjects, except possibly the Egyptians, were the early Greeks, but they were not really zoölogists. Rather, they were philosophers, interested in speculations as to the origins of things both living and lifeless, in religion, in astronomy, and in every phase of human experience. In their speculative flights they were untrammeled by any need of keeping within the bounds of fact. To them such mythological creatures as centaurs, mermaids, hydra-headed monsters, were nearly as real as were the animals from other parts of the world, known to them only through the descriptions of travelers. We must not judge these forefathers of Zoölogy too harshly, however, for they were beginners, and in many ways, scientifically speaking, mere children. All of their ideas were beclouded by superstition, legend, and folk-

lore. In this respect they were in no way different from the mass of unscientific-minded people today. One might easily list a score of popular fallacies that have long been known as such to science, but which live in the minds of the people. The scientific point of view is unnatural and hard to acquire, and few possess it even in this enlightened twentieth century. Superstition and dogmatism still blind the mental vision of vast numbers, some of whom are people of ability and many are endowed with at least average intelligence. Let us then be lenient with our pioneer zoölogists, who were as free-minded, compared with their fellow men, as are the scientists of today in contrast with the great mass of people living in intellectual bondage.

These earlier Greek writers—some of them philosophers, others poets—were members of a race of sea people. "Along the shores of the blue Ægean," says Osborn, "teeming with what we now know to be the earliest and simplest forms of animals and plants, they founded their hypotheses as to the origin and succession of life. . . . The spirit of the Greeks was vigorous and hopeful. Not pausing to test their theories by research, they did not suffer the disappointments and delays which come from one's own efforts to wrest truths from Nature." The very first problems which they tackled were the ones that are still farthest from solution: the problems of the origin of living creatures, including man. They did not lack mental audacity, but they did lack judgment. Some of their theories seem quite ridiculous today, but in a few of their ideas we see the germs of modern principles.

Thales (624–548 B.C.) had a theory that the ocean was the mother of all life; that living creatures of all sorts, even terrestrial animals, arose from the womb of the ocean. Questions as to how and why did not suggest themselves.

Anaximander (611–547 B.C.) had a vague, highly mythical idea of transformation of species. Adopting the idea of aquatic origins of all creatures, he thought that each terrestrial species was a transformed aquatic type that had acquired adaptive features necessary for land life.

Empedocles (495–435 B.C.) went much further than his predecessors in his conceptions as to the transformation of species, inquiring even into the cause of adaptive structures and the general fitness of organisms. Assuming the spontaneous generation of living creatures, he thought that at first there existed merely discon-

nected organs and parts scattered here and there. These parts of animals were attracted or repelled by the forces of Love and Hate, resulting in all sorts of weird and impossible combinations so out of harmony that they could neither survive nor reproduce. Only the sufficiently harmonious and adaptable combinations persisted and multiplied. Thus is fitness explained; and we may look upon this fairy story as a sort of vague prophecy of Darwin's "survival of the fittest" idea, one of the most striking of modern evolutionary theories.

Aristotle (384–322 B.C.) has been called the Father of Natural History. A wealthy man for those times, he was able to maintain an extensive private library and, doubtless, a laboratory. He was the first true scientist in that he adopted the inductive method: that of first securing facts and then basing his principles upon these facts. Aristotle was an original investigator. Many an animal was for the first time in human history dissected and described by him, and some of these descriptions would stand today as fair models of careful observation and inference. In spite of many errors, he had a good understanding of the structure and development of the main groups of animals, and some of his observations were so far ahead of his time that they have been confirmed only within the last century. As an example of his acumen, it may be mentioned that he discovered the fact that some sharks are viviparous and that the embryo, in a manner not unlike that of the placental mammals, acquires a nutritive connection with the membranes of the maternal uterus—facts that were rediscovered only a few decades ago by Johannes Müller.

FIG. 2. Aristotle.

Aristotle became acquainted with so many kinds of animals—about 500 species are mentioned in his writings—that he felt the necessity of classifying them. He recognized eight large groups

roughly corresponding to: 1, Mammals; 2, Birds; 3, Oviparous quadrupeds (corresponding to lizards and turtles); 4, Fishes; 5, Mollusks; 6, Crustaceans; 7, Insects; 8, Animals with shells. This was, of course, a very incomplete and inaccurate classification, but it is interesting as a first effort to develop a taxonomic system.

Aristotle reached a high level of attainment in zoölogy beyond which there was little further progress until comparatively recent times.

B. The Decline of Zoölogy

The history of zoölogical progress was profoundly influenced by world movements, and it is therefore natural enough that, when the great Greek civilization declined and ultimately collapsed, the sciences declined and collapsed with it. No zoölogical writers of consequence appeared among the later Greeks, and the Romans did little better. Even ***Pliny,*** who was considered by his contemporaries as the greatest living zoölogist, is now known to have been only an indiscriminate compiler of data—half false and half true—from the writings of his predecessors. He borrowed extensively from Aristotle and attempted to substitute for the latter's relatively scientific effort at classification a purely superficial one based on the habitats of organisms. He divided all animals into three groups—flying animals, land animals, and water animals.

The Dark Ages.—The rise of Christianity, turning the minds of man from material to purely spiritual interests, had a profoundly depressing influence upon scientific activities of all sorts. The idea became prevalent that the Bible was a universal compendium of all knowledge and that it was irreligious to make original investigations after truth. The clergy, for reasons of their own, fostered this spirit of subservience to authority and exercised a dominating influence in all matters, not merely religious but intellectual and political as well. Men ceased to think for themselves, preferring to be told what to believe. When a simple observation might readily have settled a controversy, they preferred to look up authorities on the matter in question. A series of acrimonious debates, leading almost to bloodshed, was waged over the question—How many teeth has a horse? After all of the authorities had been consulted, a freethinker finally settled the debate by looking into a horse's mouth. This, however, was considered an unsportsmanlike procedure. In those days if a person found that his own

observations were contrary to authority, he did not doubt authority, he merely doubted the accuracy of his own senses. Even today there are many who hold tenaciously to authority as against the vast accumulation of facts, easily confirmed by any intelligent person, that contradict ancient authority.

During the millennium and a half of deference to authority, we find little progress in Zoölogy. It was only in the medical schools that we find any interest being taken in Zoölogy, and even here animals were used merely as aids in understanding human anatomy. ***Galen,*** an anatomist of the second century (A.D.), came to be the authority in human anatomy, and students of medicine for centuries merely studied their anatomy from his books. Dissection of the human body was against the laws and therefore Galen had to learn his human anatomy by analogy with that of other animals. He made numerous mistakes because there are many details of human structure quite unlike those of other animals. The errors, however, became authority and were taught for centuries. Instead of doing laboratory work, the student merely listened to lectures, with occasional demonstrations upon cat or dog materials. Galen's works were read as authority and if the demonstrations failed to agree, it was explained that these particular specimens were in some way abnormal. Even today explanations of this sort are not unknown in our zoölogical laboratories.

C. The Revival of Science

Individual initiative and freedom of thought and speech had been suppressed for many centuries before release came some time during the sixteenth century. Revulsion against religious, intellectual, and political authority went hand in hand. Independent thinkers here and there throughout civilized Europe dared to step out and speak forth their views. Zoölogy, which had been confined to the medical schools for a thousand years, was destined to have its revival in connection with the teaching of human anatomy.

Vesalius (1514–1564), the father of modern anatomy, was responsible for the revolt against authority in the medical schools of Paris. While a student of medicine there, he became dissatisfied with the timeworn methods of anatomical instruction then in vogue. He is said to have pushed aside the barbers, who were hired to make the demonstration dissections, and to have performed this service himself. Subsequently, in the University of

Padua in Italy, he studied anatomy and became professor of this branch in that institution. Daring to use human material, he taught anatomy from actual demonstrations only, abandoning all previous authority. His treatises on anatomy are today so accurate in detail as to need little correction.

FIG. 3. Vesalius.

Just as Vesalius broke away from the bonds of authority in anatomy, certain natural philosophers, ***Francis Bacon*** (1561–1626) in England and ***Bonnet*** (1720–1793) in France, daring spirits in an age when daring often meant persecution and death, freed themselves from the trammels of scholasticism and gave free rein to their speculations and deductions from facts. All three played a large part in the revival of interest in the Principle of Evolution, the greatest concept of biological science.

D. Progress in Various Lines

1. *The Origin of Experimental Methods in Zoölogy*

The spirit of free inquiry soon led from the earlier observational methods of study to those of experimentation. Today we consider no hypothesis of value unless it subjects itself to experimental proof. The usual procedure is as follows: One sees in an array of data some semblance of order and one wishes to know what are the factors responsible for the observed lawful arrangement. A working hypothesis suggests itself. This is tried out upon the available data and if it is consistent with the facts it is then ready for final testing by experiment. Conditions are so arranged that such and such a result must be obtained from a given set-up of experimental conditions. If the result accords with anticipation the theory is believed to be sustained; if not, it must be modified. A science is in an undeveloped or in a mature state in proportion as it is merely observational or purely experimental.

Simple experimentation had been practiced in Zoölogy even by Aristotle, but during the Dark Ages the spirit of inquiry died, and it is to ***William Harvey*** (1578–1657) that we owe the revival of experimental methods in Zoölogy. Harvey is frequently called the founder of Physiology. To him is attributed the discovery of the circulation of the blood. In his physiological work he constantly made use of experiments and it is this method, rather than any outstanding discoveries made by him, that constitutes Harvey's chief contribution to the advance of zoölogical science.

FIG. 4. William Harvey.

2. *The Beginnings of Specialization*

Not long after the Revival of Science was fully accomplished the various workers in zoölogical fields began to specialize, some becoming systematic zoölogists, others microscopists, others comparative anatomists and embryologists. This tendency to specialize has proved a great boon in Zoölogy, since one can go much deeper into a single field than he can into many. Perhaps the earliest of the biological subsciences to attain a fairly advanced condition was that of Taxonomy, or Classification.

3. *Progress in Taxonomy*

We have seen how Aristotle made the first attempt to classify animals and how Pliny reverted to a less scientific criterion of classification. The accumulation of further facts about animals made the task of classifying them progressively more difficult, and there was a long period of confusion. It is to ***Linnæus*** (1707–1778) that we owe the bringing of order out of chaos in this field. He was the son of a Swedish clergyman. During his youth he was adjudged good for nothing as a student and was therefore apprenticed to a cobbler. Later, however, coming under the

influence of a physician, he gained an interest in biological matters and soon grew to be a man of high attainment in his chosen field of medicine. After a time, we are told, his interest in pure biology came to outweigh his love of medicine and he became professor of Natural History in the University of Upsala. Linnæus' greatest work was entitled *Systema Naturæ*, first published in 1735. It passed through twelve editions. In this book we find the groundwork of our modern taxonomic methods. Linnæus made distinct advances in several ways. His introduction of scientific terminology, his clear definitions, his precise diagnoses, and above all his perfection of the system of BINOMIAL NOMENCLATURE, mark an epoch in zoölogical advance. The custom hitherto had been to give animals merely common names like catfish, gray squirrel, earthworm. The same name was frequently applied in different regions to quite unlike species, just as today the word "pike" is used for one species in the Middle West, another species in the South, and still another in Canada. Linnæus decided to give each species a distinctive Latin name consisting of two parts, the first part being a noun indicating the genus to which the animal belonged, and the second part, usually an adjective, descriptive of the particular species. Thus he called the common dog *Canis familiaris;* the fox, *Canis vulpes;* the wolf, *Canis lupus*. Concise diagnoses and definitions in Latin accompanied each named species, so that anyone anywhere could distinguish them apart. Whenever a new species was discovered by Linnæus, he assigned it to a known genus and family or else created for it a new genus, or possibly a new family, thus definitely placing it in his system. While he greatly increased our facilities for diagnosing and classifying species, he made little progress in the discovery of the broader

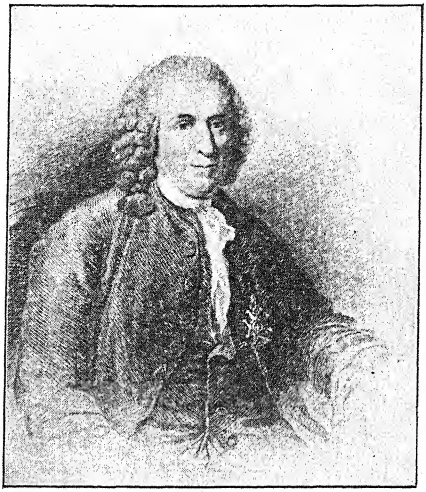

FIG. 5. Carolus Linnæus.

relations of the great groups. Six classes of animals were distinguished by him: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. This is hardly as adequate as the classification of Aristotle. Probably Linnæus' failure to see more deeply into the fundamental grouping of organisms was due to his slavish adherence to the idea of special creation. For him all species had been created essentially in their present form, except that certain hybrid types had arisen through crossing. While he did much to advance the practical methods of taxonomy, Linnæus is commonly viewed as a retarding agent because of his reactionary views on evolution. Furthermore, he set a style in Zoölogy that has had a wide vogue. The great majority of naturalists became species hunters. The one who named the most species was supposed to be the greatest man. So keen did the race for species become that old species were split up into several new ones in order to furnish material for more names. Thus taxonomic Zoölogy has come into bad repute among the experimental zoölogists. This attitude is, however, only partially justified, for modern taxonomists of the better type do not aim chiefly at species making but, rather, at a discovery of the true relationships of both older and newly discovered species.

4. *Progress in Comparative Anatomy*

We have seen that the early human anatomists, realizing that there was a close similarity of structure between man and the higher vertebrates, made use of the principle of homology without realizing its evolutionary significance. Out of this unpromising beginning arose a true science. Vast stores of anatomical facts were accumulated and needed only the genius of great organizers to give them significance and coherency. A group of able comparative anatomists attempted this task of making a system out of comparative anatomy. Among the leaders in this effort were the French zoölogists, ***Lamarck, Geoffroy St. Hilaire, Cuvier,*** and the Germans, ***Meckel*** and ***Goethe.*** During the latter part of the eighteenth century and the first part of the nineteenth the combined efforts of these men led to the formulation of certain definite guiding principles, or laws, and especially the law of the Correlation of Parts and that of the Homology of Organs. The first means that there is always a relationship of interdependence among various structures, so that changes in one part involve corresponding changes in others; the second was a greater prin-

ciple and one that underlies the whole subject of comparative anatomy.

5. *The Principles of Homology and Analogy*

An analysis of the situation showed that a distinction must be made between structural and functional resemblances. A part is homologous with another if it is similar in structure, in embryonic origin, in position relative to other parts; it may have also a similar function, but this is not necessary, for homologous structures often have the most diverse functions. On the other hand, similar or equivalent functions may be performed by organs that anatomically are quite unlike. One of the most important and difficult tasks of the comparative anatomists was that of distinguishing, in certain crucial cases, between homologous and merely analogous organs. The former are considered as evidences of relationship; the latter are believed to have no bearing on relationships, but are interesting primarily as adaptations. ***Cuvier*** (1769–1832) was probably the ablest of the early comparative anatomists and may be called the founder of that science. In addition to his knowledge of modern forms he was also conversant with fossil organisms, to which he applied the same anatomical principles as he did to living forms. It seems strange that this step did not lead him directly toward the idea of descent with modification (the essence of evolution); but he was a convinced believer in special creation and a favorite with both Church and Court. He explained the differences between the faunas and floras of the various geologic strata and their dissimilarity to those of the present by means of his Cataclysmic Theory: that there had been numerous creations, each of which had been completely destroyed and its place taken by another. Noah's flood was only the last cataclysm. Thus did the great anatomist cast the burden of his influence on the

FIG. 6. Georges Cuvier.

wrong side of the balance. He fought against the concept of evolution in debates against both Lamarck and St. Hilaire, and because of his great ability and influence succeeded in suppressing the growing evolutionary theory so that it was held in abeyance until revived by Charles Darwin about a generation later.

Today, in spite of hindrances and delays, Comparative Anatomy has come into its own as, perhaps, the chief handmaiden of Evolution and the soundest tool of the taxonomist.

6. *The Discovery of the Microscope and Its Effect upon Zoölogical Progress*

Classification and comparative anatomy depend largely upon the gross structure of animals, and much progress was made in these sciences by observing relations with the naked eye or with the aid of simple hand lenses. It was only when the need of a finer analysis of the constituents of organs and tissues became necessary that the microscope came to be employed. The problem of the finer structure of living tissues was one full of hope and stimulus to the early microscopists. They doubtless believed, as so many moderns still believe, that if they could magnify things highly enough, they would reveal the ultimate structure of living matter and thus disclose the secret of what life is. So difficult was the technical task of making adequate microscopes that some of the earlier microscopists became more interested in instrument making than in the biological end in view. Some of the earlier and better known of the microscopists were the Englishmen, ***Hooke*** and ***Grew,*** the famous Italian, ***Malpighi,*** and the Dutchmen, ***Leeuwenhoek*** and ***Swammerdam.*** Of these Malpighi (1628–1694) was probably the greatest. He wrote a famous treatise on the minute

FIG. 7. Marcello Malpighi.

structure of the silkworm and made some important contributions to histology and embryology. Leeuwenhoek is especially known for his discovery of male germ cells, spermatozoa, which he pictured without fully realizing what he saw.

FIG. 8. Antony von Leeuwenhoek.

The invention and development of the microscope gave a great impetus to the study of minute anatomy and rapid progress was made along several different lines. We now await with eagerness further great improvements in microscopes and their accessories, wondering what new things they may reveal.

7. *The Discovery of Cells*

Among the earliest results of the application of the microscope to biological materials was the discovery that all tissues are made up of small units which came to receive the name CELLS, because Hooke, the first discoverer of them, thought that they were like empty boxes or rooms surrounded by walls. This discovery was made as early as 1665, but it was not until over a century later that the significance of the discovery of the cellular structure of tissues was appreciated.

FIG. 9. Matthias Jacob Schleiden.

The Cell Principle.—Many workers, bending long hours over their microscopes, saw and figured minute organisms swimming about in pond water; others found that eggs were cells; still others that muscle fibers, skin units, and the structural units of other tissues were cells.

Although ***Lamarck*** as early as 1809 had stated in his usual somewhat vague fashion the idea that all living tissues are cellular and that growth and development are concerned with cells, it was not until 1838 and 1839 that two Germans, ***Schleiden*** and ***Schwann,*** arrived at one of the most important generalizations of Biology. Next to the Principle of Evolution the Cell Principle has had the widest influence in the development of biological science. In brief, the principle is: That all organisms are composed of cells, all of the activities of tissues are cellular activities, that growth and development, heredity and its mechanism, even evolution itself—all are affairs of cells. When the vast import of this principle came to be understood, little wonder that the majority of zoölogists for many years after decided that the study of cells rather than the study of the organism as a whole was the more promising line of endeavor. Thus grew up the clans of laboratory zoölogists, many of whom came to look upon a knowledge of microscopic technique as the chief essential for biological training and neglected to become acquainted with life in the great out-of-doors.

Fig. 10. Theodore Schwann.

8. *The Rise and Progress of Embryology*

Even before the Cell Theory had acquired its present formulation, considerable progress had been made in comparative embryology. Even Aristotle had made out with the naked eye some of the salient features of embryonic development. It is to ***K. E. von Baer,*** however, that we owe the scientific beginnings of embryology. His classic treatise on the development of the chick appeared in 1832. He is the founder of the "germ layer theory" of development, by which is meant that the whole organism is developed from the elaboration of certain embryonic cell layers, which, by foldings, irregular-

ities of growth, and thickenings produce all of the structures of the body.

Preformation and Epigenesis.—One of the most persistent and time-honored controversies of zoölogical science arose out of a study of embryology. It was known that every organism is to be traced back to a one-cell stage, the egg. The question naturally arose as to whether the egg contains within itself a representative of each organ of the adult, or whether the egg was undifferentiated at the beginning and only acquires differentiated structures during the course of development as the result of functional activities. The PREFORMATION IDEA is in its earliest form totally unacceptable. The egg was believed by the extreme preformationists, such as *Bonnet,* to be merely a very much shrunken and condensed organism that needed only to feed and expand in order to unfold into an adult. The EPIGENESIS IDEA as proposed by *Wolff* was that an egg, such as that of a hen, was at the beginning a homogeneous mass of living substance and that organs gradually differentiate out of it *de novo.* No one today holds to either of these views to the exclusion of the other, but it is the modern orthodox opinion that development is the result of a certain inherited, therefore predetermined, germinal constitution influenced at every step by environmental and functional factors. The main controversy at present seems to center about the problem of the relative potency of heredity and environment in the determination of individual development.

FIG. 11. Karl Ernst von Baer.

Experimental Embryology.—So long as embryology remained purely observational it did not throw much light upon the mechanics of development. Fortunately, however, embryology and its cousin-science, cytology, rapidly became experimental, and the results have been most illuminating. This phase of embryology and cytology has come to be known as the Physiology of

Development (*Entwicklungsmechanik* of the Germans). The problems that confront experimental embryology are of extreme difficulty. We know that the egg must contain within itself the potentiality to become an adult, but we do not yet know the nature of this potentiality. Some hold that every adult difference is represented by a minute organic particle in the chromatin of the nucleus; others hold that the egg cell is merely a fairly simple reaction-system and that the environment determines the course and the consequences of development. Experimental methods of analysis involve the alteration of various environmental relations, one at a time, and the results are then compared with those seen under normal conditions. Comparative studies of results obtained in related and in unrelated groups are made, and generalizations as to how much of development is due to hereditary factors and how much to environmental factors have been deduced; but the main problems of experimental embryology remain still unsolved.

FIG. 12. Gregor Johann Mendel.

9. *The Rise and Progress of Genetics*

One of the direct results of the adoption of the experimental method of studying development was the birth of the modern science of Genetics. The first great step was taken by ***Gregor Mendel*** (1822–1884), a man who appeared a generation before the world was ready to receive his message. He studied the processes of development and heredity at first hand. He was not interested in any theories of evolution nor in any controversies as to preformation and epigenesis. All he wanted to know was something exact and definite about the rules according to which offspring repeat the characters of their parents. Using simple, easily controlled materials (common garden peas) he worked out the celebrated Laws of Heredity that bear his name. Today Mendelian Heredity forms the heart and core of modern genetics, which in turn is, per-

haps, the liveliest phase of modern Zoölogy. What a profound effect a knowledge of Mendel's findings would have had upon the evolutionary conceptions of Charles Darwin! Darwin, however, never knew of Mendel's work; in fact, no one seems to have known anything about Mendel until 1900, sixteen years after his death, when his work was rediscovered. Now his name has become a household word almost as familiar as that of Darwin.

10. *Progress in Evolution*

We have seen that the beginnings of the evolution idea go back beyond the dawn of scientific Zoölogy, appearing in the speculations of Greek natural philosophers as to the origins and transformations of living things and culminating in the relatively elaborate evolutionary conception of Aristotle.

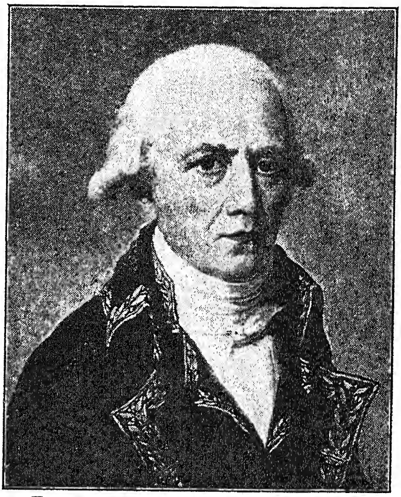

FIG. 13. Jean-Baptiste Lamarck.

After Aristotle the evolution idea made no progress for many centuries. Even after zoölogists had developed a considerable knowledge of classification and comparative anatomy, a fair comprehension of the cell principle, and some experience in embryology, they continued to hold to the special creation doctrine. Species were looked upon as fixed or constant, each created in the form in which it is now found. One after another, however, zoölogists became dissatisfied with a static conception of the world and came to adopt the idea of a changing world, an evolving world. Although a number of philosophers had expressed evolutionary convictions, it remained for ***Buffon*** (1707–1778) to put evolution on a naturalistic basis; hence he is called the founder of the modern applied form of evolution. His ideas, however, were far from clear and he finally retracted them altogether under pressure of the Church authorities. ***Erasmus Darwin*** (1731–1802) published in his classic volume, *Zoönomia* (1794), a complete theory of evolution, which

was a partial anticipation of the principal views of Lamarck. His concepts were largely deductive and unsupported by any adequate body of facts. ***Lamarck*** (1744–1829) was perhaps the most important figure between Aristotle and Charles Darwin. His theory of *The Inheritance of Acquired Characters* as a causal explanation of adaptation is still held by a growing minority of modern zoologists. The essential features of his theory are: first, that all structures of an individual are modified by use or disuse and by changing environment; second, that changes in the body thus produced are passed on by heredity to offspring. Whether or not Lamarck was right is still unsettled. This is one of the oldest and most acrimonious of biological controversies.

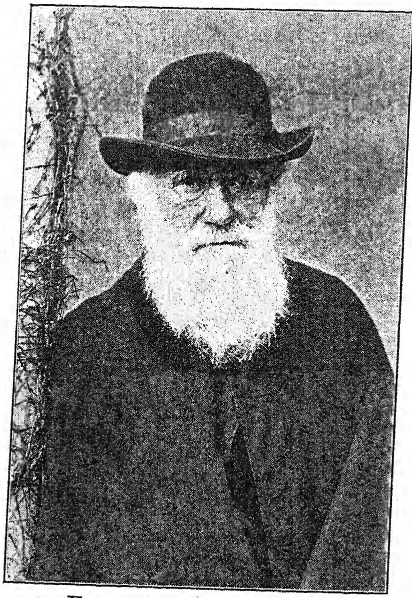

FIG. 14. Charles Darwin.

Lamarck was strongly opposed by his eminent contemporary, ***Cuvier,*** who, though his own discoveries furnished strong evidence of evolution, continued steadfastly to the end of his life a special creationist. In a famous debate in the French Academy in 1830, Cuvier and ***Geoffroy St. Hilaire,*** a leading zoölogist and champion of Lamarck, argued the question at great length. Cuvier was adjudged the decisive winner. This decision was a serious blow to the evolution theory and served to check further development along evolutionary lines for nearly thirty years.

Charles Darwin (1809–1882).—The most striking figure in zoölogical history is Charles Darwin. Barely twenty-one years of age at the time of the great Lamarckian debate just referred to, he had not yet seriously entertained the evolution concept, but after reading ***Malthus' On Population*** and ***Lyell's Principles of Geology,*** and especially as a result of his journey around the world in the ship, *Beagle*, during which he accumulated a great mass of data, he became convinced of the truth of the evolution idea and set about

proving it. This he did by means of a vast array of facts which support and agree with the theory. He also offered as an explanation of the cause of evolution his famous theory of *Natural Selection,* or survival of the fittest, a theory held at the present time to be of secondary importance, though valid within certain limits. Darwin's first large publication was his famous *Origin of Species* (1859). This book stirred up an immense amount of controversy. It was bitterly opposed by churchmen in general and ardently supported by scientists. ***Huxley*** (1825–1895) was the leading advocate of Darwinism and is credited with a complete victory over the supporters of special creation. For many years there was no further serious opposition to the general principle of evolution, but there is no general agreement even yet as to the causes and methods of evolution. These are hard problems that will yield only to long and arduous investigation. That we do not know exactly the causes of evolution is no valid reason for doubting so well established a principle. As well doubt the fact of individual development, or that of heredity, because we do not know exactly their causes or mechanisms.

FIG. 15. Thomas Henry Huxley.

SUMMARY

The history of Zoölogy has been traced from its crude beginnings, through its many vicissitudes, its ups and downs. It has had an evolution much like that of an organism or a group of organisms. It has become split up into a number of subordinate special sciences, like the species of a genus. Some of these subsciences have proved more fruitful and more important than others and have added prestige to the group as a whole; others have only begun to gain a foothold. Each part has some connection with all others, just as each species in a given ecological complex is more or less dependent upon others and all are parts of a great delicately balanced system. We cannot follow all the branches at once but must in the future isolate them, one after the other, for special treatment.

It has been suggested that we add to this chapter a section on the history of American Zoölogy. This suggestion has been carefully considered, but has not been accepted, because American Zoölogy is a matter of relatively recent development. Most of the real leaders in the field are still living and active and hence are as yet hardly historical figures.

PART II

GENERAL BIOLOGICAL PRINCIPLES

[illegible]

CHAPTER III

LIFE IN ITS COSMIC SETTING

A. The Cosmos and Its Units

The term COSMOS is in a sense synonymous with the term UNIVERSE, but carries with it the further implication that the universe is organized in an orderly fashion. Orderly organization is a prime characteristic of nature and is its most important attribute. Order is maintained constantly in spite of continual change and apparently disorderly local disturbances.

The basis of organization in the cosmos is that it is an immense unit composed of a series of smaller units, all organized into an orderly system. These secondary units are again composed of tertiary units arranged in orderly fashion and interrelated in their activities in such a way that each of them behaves as a whole. Tertiary units are again composed of smaller units similarly organized into wholes. The various wholes we speak of as UNITS. These units may be regarded as constituting a progressive series of levels of organized unity. Assuming that the whole cosmos is one inconceivably immense unit, we may think of it as composed of a system of supergalaxies. Each supergalaxy is thought to be composed of an immense number of galaxies, and each galaxy of millions of stars, which are of the same order as the Sun. Each star, or sun, is the center of a group of planets, and many of the planets have about them one or more satellites. So the units of the cosmos may be listed in descending order as the cosmos itself, supergalaxies, galaxies, stars, planets, and satellites.

B. Our Solar System and Others

Starting in with our own solar system as an example of the most familiar and perhaps fundamental of the cosmic units, we find that its organization is as follows: In the center is the great hot ball, the SUN, which has a diameter of approximately 1,000,000 miles. At its surface the Sun is composed of matter in a superheated gaseous condition, the surface temperature being about 10,000° Fahrenheit. In the center of the Sun matter must

be enormously hotter than this and, being under tremendous pressure, must be solid or supersolid. The Sun revolves on its own axis and about it circle the planets at immense distances. As compared with the Sun, the PLANETS are very minute bodies whose aggregate mass is only about one seven-hundredth of that of the Sun. The largest of the planets, Jupiter, has a diameter of about 88,000 miles, which is about one tenth that of the Sun and about ten times that of the Earth. The major planets, Mercury, Venus, the Earth, Mars, Jupiter, Saturn, Uranus, and Neptune circle in orbits about the Sun, the orbit of Mercury being the closest and that of Neptune being the furthest away. Each of the planets has its own special density, speed of rotation, surface temperature, etc. None of them are very much like the Earth in these respects. The Great Planets have circling about them many SATELLITES, Jupiter and Saturn having nine each, while the smaller planets have only one or two satellites. In addition to the eight major planets there are known to exist over a thousand small planets ranging from about 200 to 500 miles in diameter to very small ones about 25 miles in diameter.

In order that the student may have a definite idea as to the differences found among the planets the following table, taken from *F. R. Moulton*, is introduced.

Planet	Distance from Sun	Mean Diameter	Density (Water = 1)	Mass (Earth = 1)
Mercury	36,000,000 miles	3,009 miles	4.5(?)	0.05(?)
Venus	67,200,000 miles	7,701 miles	4.9(?)	0.81(?)
Earth	92,900,000 miles	7,918 miles	5.53	1.00
Mars	141,500,000 miles	4,339 miles	3.58	0.11
Jupiter	483,300,000 miles	88,392 miles	1.25	314.5
Saturn	886,000,000 miles	74,163 miles	0.63	94.1
Uranus	1,781,900,000 miles	30,193 miles	1.44	14.4
Neptune	2,791,600,000 miles	34,823 miles	1.09	16.7

This great system with its central Sun goes on age after age maintaining essentially the same relationships part to part. The movements of each part are regulated by the masses and motions of all the others and especially by those of the Sun. No unit is

independent of any of the others and the whole system behaves as a unit.

A solar system may be regarded as perhaps *the* fundamental unit of organization of the cosmos, comparable in a sense with the CELL as the fundamental life unit and the ATOM as the unit of matter, for each is composed of smaller units and aggregations of each go to make up larger units. The familiar Sun is really a star and the stars are solar systems, suns with families of planets. About 5000 of these star-suns are visible to the naked eye, but the telescope reveals the presence of hundreds of millions of more distant stars quite comparable in size with the nearer ones. Some of these star-suns are much larger than our own solar system, Betelgeuze being about 27,000,000 times as great in volume as our Sun. Some star-suns are, however, smaller than the Sun. The Sun is then to be regarded as a star of intermediate size, perhaps below the average of the whole group in relative importance. Although they seem to our defective vision to be close together, these star-suns are immensely far apart. According to Moulton, "if a sphere having a radius of 200,000 times 100,000,000 miles were constructed with its center at the Earth, it would contain within its interior no star except our own Sun."

C. Our Galaxy and Others

The astronomer finds that miles as units of measurement are far too small for his purposes. He needs a much larger measure. For convenience he has adopted for his measuring stick the "LIGHT YEAR." Now light travels at the rate of about 186,000 miles per second; hence if we multiply this number by the number of seconds in a year, we obtain a figure beyond the human imagination, "the light year," which is approximately 6,000,000,000,000 miles. *Alpha centaurus* the nearest star-sun to our own system, is about four light years distant. The North Star is 40 light years away, and others are 300 or more light years away. All of these star-suns are arranged in the form of a great star-cloud called a GALAXY. Our own galaxy is shaped somewhat like a watch and we are located far in the interior of it. When we see the Milky Way we are looking out toward the edge of the disk. Thus we see more star-suns when we look through the wide diameter than through the narrow diameter of the disk. All the stars in our galaxy have regular motions among one another, but they rarely come close

to each other for they have so much room in which to move. It is as though one fly in New York, another in Chicago, another in San Francisco were to start flying about the world and kept it up for a million years or so. The chances of their meeting would be excessively small.

The galaxy then is a larger unit composed of the fundamental units called star-suns organized into a finite group, which acts as a whole. Astronomers tell us that within the range of their telescopes are hundreds of thousands of SPIRAL NEBULÆ and GLOBULAR STAR CLUSTERS, which they believe to be exterior galaxies, comparable to our own galaxy in size and complexity. Some of these galaxies are so far away that it takes light 1,000,000 years to travel from them to us. That means that the light which just now comes through the telescope started from these units 1,000,000 years ago and has been traveling at the rate of 186,000 miles per second ever since.

Whether or not these galaxies are the largest units making up the cosmos, we do not know. Some astronomers believe that a group of perhaps millions of galaxies are organized into a supergalaxy and that there are other supergalaxies. Speculation along these lines tends to induce mental dizziness, so let us desist and go no further.

D. The Earth as the Abode of Life

One finds it difficult to come back to a consideration of so small and trivial an object as our own Earth, a second-rate planet belonging to a second-rate star-sun, among the millions of other star-suns in one of perhaps a million galaxies. But it is necessary to come down to earth if we are to study biology, for all the biology we know is derived from the study of the thin film of life units distributed over the surface of one little planet.

Does Life Exist Elsewhere than on the Earth?—It is easier to ask this question than to answer it. It would seem that life might exist on other planets of our own solar system, but even if we decide against this possibility there are plenty of other solar systems with millions of other planets, some of which must be much like the earth in size, temperature, density, and climate. The consensus of opinion of astronomers seems to be that none of the other planets of our own solar system afford a suitable home for life. Some are far too hot, others far too cold. MARS is believed by astronomers

to possess a very thin atmosphere of water vapor, which condenses into a thin layer of frost at the poles. What little oxygen it may once have had is believed to have combined with the surface iron to produce red rust—hence the red color of the planet. VENUS, the planet most nearly like the Earth in size, has been found to possess a fairly thick atmosphere of almost pure carbon dioxide. It too, if it ever possessed an appreciable amount of oxygen, has used it up through surface oxidation. JUPITER and SATURN have abundant atmospheres but their chief constituents appear to be ammonia and methane, substances harmful to life, and if oxygen be present at all it must be in a rarified state in the upper atmosphere. So it appears that there is something radically wrong with all the other planets in our solar system from the standpoint of their suitability to be abodes of life.

The Special Fitness of the Earth as the Abode of Life.—The Earth is peculiarly adapted for life in a multitude of very special ways. It has just the right mass to hold an atmosphere of the gases most essential for life and to hold an aquasphere, which is at least mainly in the liquid state. It has a temperature range at the surface covering only a tiny fraction of the total temperature range, a range relatively close to absolute zero and one in which many chemical unions important for life are possible and in which many complex chemical molecules are relatively stable. Later on we shall see how important these special properties are for the existence of life. We see that we would be expressing a very one-sided view of nature if we were to speak of living things being well adapted to or fit for their environment. It is equally significant that the environment is peculiarly and eminently well adapted for living things. Change the environment only a little and life would disappear and new life could not reappear.

So we may regard the Earth as *the* home of life and perhaps unique in life supporting properties, at least among the planets of our solar system.

For our purposes we have gone far enough into the study of cosmic units. Let us now examine briefly some of nature's smallest units.

E. UNITS OF MATTER AND ENERGY

Atoms.—In about the same sense that star-suns may be regarded as the most fundamental of cosmic units and cells as the most fundamental of life units, atoms may be regarded as the most

fundamental units of matter. All matter on earth is composed of atoms, of which only 92 different kinds are known. Each kind of atom has its own peculiar set of properties and no two have the same characteristics. There are atoms of hydrogen, of oxygen, of iron, of sulphur, of chlorine, of carbon, of gold, of radium, etc., each of which has many unique properties which are the result of the internal organization of the atom itself. An atom of oxygen, for example, is very much like a miniature solar system, for it consists of a central nucleus like a sun and has revolving about it a group of planet-like bodies known as ELECTRONS. The nucleus of an atom is made up of a definite number of minute particles known as PROTONS, ELECTRONS, and NEUTRONS. The protons are positively charged, the electrons negatively charged, and the neutrons electrically neutral. The number and arrangement of these elementary particles differs in each kind of atom, and the number of planetary electrons, though constant for each kind of atom, vary regularly from atom to atom in a systematic way. The physical properties of an atom seem to be largely due to the make-up of the atomic nucleus, while the chemical properties result from the numbers and arrangement in orbits of the planetary electrons. If by drastic bombardment any particle is removed or added to an atomic nucleus, the physical characteristics of the atom change and, similarly, if any planetary electron is gained or lost, the chemical properties change.

The atoms vary in size from element to element, but all are almost inconceivably small. The atom of hydrogen, the smallest of atoms consisting of but one proton as a nucleus and one planetary electron, is enormous as compared with the size of its proton and electron. "If," according to ***Lemon,*** "this tiny system were to be magnified so that its orbit would be 1,000 times the size of the orbit of the Earth around the Sun, the electron would be approximately the size of the Sun and the nucleus (the proton) approximately the size of the Earth; and the analogy to a little solar system, therefore, while comparable as to relative magnitudes of the objects involved and the size of their orbits, is a peculiar topsy-turvy affair with respect to the size of its components, because the large, but light, electron revolves about the comparatively small, but heavy, nucleus." Like the solar system the little atomic system is very largely empty space.

As to the actual size of atoms, electrons, and protons we may say

that the total diameter of an atom of hydrogen is 10^{-8} centimeters, that of an electron 10^{-13} centimeters, and that of a proton 10^{-15} (?) centimeters, which means roughly that three billion atoms side by side could be placed in a line across the diameter of half a dollar, while protons are a million times as small. Dimensions so small as these are as staggeringly inconceivable as are the vast dimensions of cosmic objects such as galaxies and supergalaxies. One is as conducive to mental vertigo as the other. Even the largest atoms such as those of the heaviest metals, Thorium and Uranium, are of the same general order of magnitude as is the atom of hydrogen.

Whether the protons and electrons are the ultimate units of matter and energy is not known, but some physicists have expressed the suspicion that even they may be systems made up of still more minute entities. A modern theory concerning light and other forms of radiant energy holds that they are composed of particles called photons. These may possibly be the smallest of nature's units.

F. Nature's Scale of Magnitudes

Ranging from the magnitude of the largest cosmic units down to that of the smallest known units of matter there are size differences almost inconceivably great, but the gap between extremes is bridged by a series of magnitudes of less startling dimensions. We have below the galaxy level, a wide range of star-sun dimensions, and below these planet dimensions ranging down to tiny planets of 25 miles in diameter. No doubt these grade down to much smaller objects. Working up from electronic and atomic dimensions we find that organized groups of atoms form MOLECULES that are immensely larger than atoms though still ultramicroscopic in size. Molecules form CRYSTALS that are large enough to be seen with the naked eye, and COLLOIDAL PARTICLES considerably below the level of unaided vision but still much larger than molecules. Aggregations of crystals form mineral masses of various sorts in which there seems to be some slight degree of organization, but in which no definite units are distinguishable, for the masses are shapeless and have no size limitations.

G. The Relative Dimensions of Life Units

The units of life ranging from the gene to the largest organisms such as the giant sequoias and the whales occupy a zone in the

scale of dimensions about midway between that of the galaxies and that of the protons and electrons. A microscopic bacterium would appear about as large to a proton as would a galaxy to a man. A mathematical friend of the writer once took the trouble to make out for him a scale of dimensions ranging from galaxies to protons and we were surprised to find that man and microbe belong essentially to the same scale of magnitude and that this scale occupies a median position in the total dimensional scale. Strange as this may seem, we are forced to the conclusion that life units are in one sense extremely small, but in another sense tremendously large. Life units then occupy a rather unique position about midway between the giants and the pygmies of nature's units.

H. The Philosophy of Organized Units

Every science has a basic or underlying philosophy which helps to unify and clarify our broader thinking about our fields of interest. In modern times philosophers have given us an illuminating concept about the units of the universe that has received various names, such as *holism*, the *organismal theory*, and the *emergence theory*.

According to these views any complex unit is to be regarded as an organized whole composed of minor parts; such a whole has certain properties that are not merely equal to the sum of the properties of the parts but are new and unique properties of the whole resulting from the peculiar organization of the parts. Let us take for example a very simple system, the molecule of water, consisting of two atoms of hydrogen and one atom of oxygen. Hydrogen and oxygen atoms each have their own unique physical and chemical properties, but these properties disappear and a whole new set of properties emerge as though created out of the blue when two atoms of hydrogen and one of oxygen unite to form the higher unit, the water molecule. Water has a score or more new properties that are the resultant of its new molecular organization and are not to be understood as the sum of the properties of its parts, unless we include among the properties of oxygen and hydrogen those that emerge in their combinations with each other.

Again, when water molecules unite in their characteristic way to form beautiful and elaborate snow crystals, the latter are units of a still higher level and possess many new properties of the whole that are not expressed in the countless individual water molecules that went to make up the crystal.

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There are unique properties of atoms that are due to the number and organization of their contained electrons and protons. And doubtless there are properties of a galaxy that are more than the sum of those of its contained stars.

As we shall see in more detail in Chapter VIII, life units such as cells and organisms are composed of many kinds of molecules, but these ingredients do not in themselves account for the special vital properties of these living units. The special and peculiar properties that distinguish living units from all others are a consequence of a unique type of combination and organization of ingredients which in themselves are not alive. Life may be regarded then as a set of properties that emerges when a certain level of organization has been reached. Life units themselves may be relatively simple or relatively complex. The simplest units have simpler properties and more complex units have new and different properties. Whenever simpler life units are combined and organized to form larger and more complex life units, new properties emerge with each higher step in organization.

The ideas just expressed are embodied in the EMERGENCE THEORY or the THEORY OF EMERGENT EVOLUTION. The particular application of this theory that concerns us in the immediate future is in connection with the next chapter where we shall discuss the special properties of living units. The explanation of these properties is not to be found in an analysis of the properties of the ingredients, but may be regarded as new properties emerging with the particular type of organization found in the unique levels of natural unity found in the life units themselves. From this point of view there is no more mystery about the origin of life than about the origin of the water molecule. In both types of unit new and special properties emerge as the direct result of a new and special organization of lesser units into greater units.

Our purpose in this chapter has been to help the student to get his mental bearings in the universe of which he is a part, to aid him in acquiring a cosmic perspective about himself and other living creatures, to make him realize that even the tiniest living unit is large enough to be immensely complex in its organization. We realize that much of what we have written is far off the beaten track followed by textbooks of biology, but it is time some one broke away from tradition in this respect.

SUMMARY

1. All nature is a vast organized cosmos composed of units of various levels of complexity.
2. The galaxy is the largest of the known units of the cosmos. A galaxy is an organized group of millions of star-suns.
3. A star-sun, or solar system, such as our own, is the center of organization of many planets, planetoids and satellites.
4. It appears that in our solar system no other planet than the Earth possesses the physical conditions necessary to support life.
5. The Earth is uniquely fit to support life.
6. Atoms are the fundamental units of matter.
7. There are ninety-two different kinds of atoms.
8. Atoms are organized to form units of a higher order, called molecules.
9. Atoms consist of units of energy known as electrons and protons, respectively particles of negative and positive electricity.
10. In nature's scale of magnitudes it appears that life units, ranging from microscopic bacteria to whales, occupy a section of the dimensional scale midway between that of galaxies and that of electrons.
11. The theory of Emergent Evolution holds that the properties of complex units are more than the sum of the properties of the contained parts; that new properties of the whole emerge as a direct consequence of organization of parts.

CHAPTER IV

LIFE AND THE PROPERTIES OF LIVING UNITS

A. What Is Life?

Most of us think we know what life is, but if asked to define life we find ourselves confronted by an almost hopeless task. Even the dictionaries and encyclopedias whose function it is to define terms, fail dismally in their efforts to define the term "life." One dictionary defines life as "the state of living," but leaves us in the dark as to what "living" is. Another dictionary defines life as "the sum total of vital functions," but leaves us to guess the meaning of the term "vital." The real difficulty is that the term "life" is an abstraction without any objective reality and therefore evades definition. We can speak correctly of living organisms, for such things exist, but "life" apart from living units does not exist and therefore it is no wonder that we cannot define it.

The Realities of Biology Are the Life Units.—Realities can be defined in terms of their peculiar properties. In most of our textbooks and treatises of biology we find frequent reference to a substance known as protoplasm, the so-called living substance, the properties of which are commonly listed and combined to make up a definition of "life"; but the term "protoplasm," like the term "life," is more or less an abstraction. Protoplasm has no separate existence in itself, but is merely a term for the complex of organized materials that make up living units.

The life units are the tangible entities with which we have to deal and these units have certain properties in common that are characteristic of the living state. When we have stated the unique properties of living units we shall have defined the abstract term "life" in an indirect and round-about way. And this is the only way in which we can arrive at a definition of life.

B. The Characteristic Properties of Living Units

Living units possess a certain set of properties or characteristics not possessed by any nonliving unit. Some lifeless units may pos-

sess one or more of these properties, but none possess them all. It is in the possession of a certain unique combination of properties, then, that living units are different from all other natural units. The following list of the properties of living units will serve to introduce briefly a number of important topics for further elaboration in subsequent chapters.

1. Life Units Are of Definite Size and Shape.—Living units are never formless masses like clouds or bodies of water, but are discrete masses, each kind of unit having a specific range of size, a definite shape, and a definite internal organization.

2. Life Units Tend to Form Aggregates.—At every level of unity single life units tend to unite more or less closely to form one sort or another of social units, or animal aggregates. The extent to which the social forces result in integrating these aggregates into units of a higher grade varies from group to group. It should be emphasized here that throughout the living world there is a deep-seated tendency for units to coöperate for mutual benefit. This subject is discussed in Chapter V and in many other connections throughout the book.

3. The Chemical Constitution of Life Units.—Certain complex chemical substances are invariably found in the elaborate structure of living organisms. The most unique of these substances are carbohydrates, lipins (fat-like substances), and proteins, the most complex substances known. In addition to these peculiarly organic substances living things are made up largely of water and contain many common inorganic salts, all of them substances that are most abundant and widely distributed throughout the environment.

4. The Intimate Physical Structure of Living Units.—The keynote as to the physical peculiarities of living material is struck when it is stated that the active material in living units exists as a COLLOIDAL SYSTEM. Many of the properties of living things depend upon the colloidal character of the materials of which they are composed.

5. Metabolism—the Energy Traffic in Cells.—So striking a feature of living things is metabolism that some have gone so far as to state that "life *is* metabolism." Only by stretching the term beyond its ordinary meaning can such a statement be defended. However, life cannot go on if metabolism ceases, for with the cessation of metabolism the organized unity of cells breaks down

and even the colloidal character of the material becomes disorganized.

6. Growth—Increase in Size of Units.—All living units have the capacity to grow at the expense of nutritive materials expropriated from the environment. Each type of unit increases in size up to a fixed and rather definite size limit beyond which it will not go. The method of growth differs from that of nonliving units such as crystals in that it takes place through INTUSSUSCEPTION, i.e., by the increase of every minute part of the active material; while in crystals and other nonliving units growth is a matter of merely adding material to the outside. Growth in living units is seldom if ever a mere matter of increase in size. With increase in size there is usually change in internal organization, which we call DIFFERENTIATION.

7. Reproduction.—All organisms have the power of producing more organisms of their own kind. In all cases the method of reproduction involves the isolation from the body of the parent of some representative portion of the latter. This holds whether the isolated part of the parent is half of itself or a single cell out of billions present. The point is that the essential organization of the parent type is present potentially in the isolated part and that the latter has the power to reproduce the full adult form of the species to which the parent belongs.

8. Heredity.—Through the processes of reproduction offspring are produced which tend to resemble the parents in general organization and in many finer details of structure. The various individual differences between the two parents (when reproduction is biparental) are distributed among the offspring according to certain well understood laws, already referred to as Mendel's Laws. Chapter XLVIII is devoted largely to a consideration of this topic.

9. Variation.—Though offspring tend to resemble parents in a general way, no offspring is a true duplicate of either parent and no two offspring of any pair of parents are exactly alike. In fact, no two members of a species are alike in all details. This universal variability of individuals is one of the most remarkable features of living organisms and constitutes a main factor in evolution. The various modes and methods of variation are dealt with at some length in Chapter XLVIII.

10. Development.—Another peculiarity of life units is that after

a new unit has been given off from an old unit—a process which we have called reproduction—the new unit does not merely grow in size, but goes through an orderly succession of changes leading finally to a nearly complete duplication of the structural and functional features of the parents. Even such a very simple organism as a Paramecium exhibits development. After two offspring are produced by the transverse division of a parent individual, they are at first unlike each other and unlike the parent, but each goes through a series of orderly changes as it grows up into the "adult" condition.

11. Responsiveness.—All living things are sensitive to changes in their environment and are continually responding to stimuli that come from the outside or from within their own bodies. Lifeless things also respond to stimuli, but living things are excessively responsive and react in far more complex and varied ways than do lifeless things. Different parts of an organism respond in different ways to different kinds of stimuli. Responses to stimuli may involve changes in form, movements of parts, movements of the whole organism, or in the chemical intake or output of cells. The study of stimulation and response constitutes the main subject matter of physiology and of animal behavior.

12. Coördination and Integration.—In all except possibly the very simplest life units there is a tendency for the various specialized parts of the unit to act in harmony with one another. The real test of whether a life unit is fully an organism, and not merely an aggregate of independent parts, is its possession of the power to coördinate and unify the activities of the various parts so that the unit behaves as a single individual. The various types of coordinating and integrating mechanisms are discussed in a separate chapter (Chap. XXXIX).

13. Adaptiveness.—One of the most remarkable properties of living organisms is their ability to respond to stimuli adaptively. By this we mean that growth responses, behavior responses, and other responses, are usually of a beneficial sort, so far as the organism is concerned. Not all responses are favorable to the individual but most of them are favorable at least to the race. A special chapter is devoted to a discussion of adaptation (Chap. XLI).

14. Variety and Unity of Living Forms.—One of the truly remarkable characteristics of living things is that there are such tremendous numbers of different kinds of animals and plants. Yet

a sort of underlying unity pervades this variety, for all have many characteristics in common. Moreover there is a marked tendency for the different kinds of organisms to resolve themselves into groups, the members of one group having more characters in common among themselves than they have with members of other groups. There is therefore a sort of natural grouping of organisms into larger and smaller subdivisions according to their resemblances and differences. A study of this natural grouping of living things is the function of that branch of biology known as TAXONOMY and is dealt with in Chapters XII and XIII.

15. Evolution.—A final attribute of living things is that they tend to change their forms and functions over long periods of time, the changes in general being in the direction of increased efficiency in living. In other words, the forms of organisms are not static, but dynamic, changing slowly from age to age. This property of living things finds expression in the term ORGANIC EVOLUTION, a phenomenon dealt with at some length in the last part of this volume.

This brief outline of fifteen of the outstanding characteristics of living units will serve as a logical plan for the treatment of biological facts and principles. With these twelve topics as starting points, it should be possible to write a comprehensive treatise on biology that would omit few matters of real significance.

Some of the properties listed above, especially Nos. 1, 2, 3, 4, 5, and 14, are considered as good orientation material, best presented before introducing representative types or groups of animals. The remaining properties in this list are more likely to be intelligible after the study of animal types has been completed, for the characteristics of the animals themselves should be known and used to illustrate the principles involved in these topics. Some of these properties of living units, however, will be best illustrated along with the study of the types themselves in whatever connection they seem to fit in most appropriately.

This then is the plan on which this book is written. The student is the best judge of its adequacy.

SUMMARY

1. It is futile to attempt to define "life," for the term is an abstract concept. Life has no existence apart from living units.

2. The real entities are living units of varying levels of complexity of organization.

3. The term "protoplasm" is also the name of an abstract concept. It is no more than a convenient general label for the organized substances making up living matter.

4. Life, if definable at all, can be defined only by listing the characteristic properties of living units.

5. Fifteen characteristics of living units are listed and briefly commented upon. These properties are to be the subjects of chapters throughout the whole book.

CHAPTER V

ORGANIZED UNITS OF LIVING MATTER

Organization the Fundamental Feature of Life Units.—By far the most important fact about living things is that they exist in the form of organized units of various levels of complexity. The fact that organization is the keynote of life must have been foremost in the mind of the first man who applied the term "organism" to a living being. When we say that anything is organized we imply that it is complex and composed of many parts that might be conceived of as existing in a disorderly fashion, but actually do exist in an orderly state. An organism then is a complex system of many parts so arranged and so harmoniously interacting that it behaves as a coherent whole.

The Various Levels of Life Units.—Several different levels of life units are recognized. Foremost among such units are those variously known as *individuals*, persons, or organisms. It is difficult to define exactly what an individual is, biologically speaking. A dog is an individual, a man is an individual, and some single cells such as an Amœba, a bacterium, or a unicellular plant are individuals. In other words, an individual is an independent unit fully separated from others and able to move about by itself and carry on a personal life free from others of its kind. It is a separate individual whether it be composed of one cell or many cells, of one multicellular unit or a group of multicellular units. The individual level of unity is to be regarded as the most fundamental level of life units.

Rivaling the individual for supremacy among life units is that unit known as the CELL. Many biologists consider the cell as the basic unit of life, even more fundamentally significant in some ways than the individual. Around this view that the cell is supreme has grown up an elaborate concept called THE CELL THEORY, which holds that all living things are composed of one or more cells and that "the functions of the body in health and disease are but the expressions of the activities of the individual cells" making up the body. This conflict between the "individual" and the "cell" for primacy among life units is expressed in the rival schools of OR-

GANISMALISTS and ELEMENTALISTS, the former supporting the primacy of the individual as a whole, the latter that of the cells.

Several levels of units, some below and some above the cell and individual level of units, are believed by many biologists to be as truly units as are the latter. Some recent writers emphasize the importance of genes and viruses as subcellular units and most biologists consider that closely knit societies of individuals constitute true life units. Let us consider the question as to whether these entities deserve to rank as life units.

Are Genes and Viruses True Life Units?—Later on in the course much will be said about genes. For the present we can picture them only vaguely. A GENE is a discrete and semi-independent, self-perpetuating particle that carries on its existence among other genes as part of a cell. Each kind of gene is a relatively stable particle that may be no larger than a single large molecule and each gene is specifically different from other genes. The special function of genes is to carry from generation to generation certain specific potencies that express themselves in the specific hereditary characteristics of the individual. The reality of genes cannot be successfully challenged, but it is extremely doubtful whether they deserve to rank as definite life units of greater significance than other parts of cells.

VIRUSES are entities that have some claims to be regarded as independent life units. No one has yet seen a virus unit, but they are believed to exist because they behave somewhat like disease-producing bacteria. The disease known as small-pox, for example, is due to an invisible something that is transmissible from individual to individual, that produces certain specific damaging effects, that grows and produces more of itself in the bodies of its victims. If it is made up of discrete particles the latter are so minute that they have never been seen through the microscope and they pass through the pores of our finest filters—hence the name FILTERABLE VIRUS. Because they behave essentially like disease-producing bacteria, they are regarded by some as ultra-minute bacteria-like units. Another view about them is that they consist of substances in solution and are not organized units at all. Very recently the active substance of a virus has been isolated in crystalline form and has proved to consist of protein. Calculations as to the size of virus units, assuming that they *are* really separate units, have been made on the basis of size of the pores in filters. Such calculations have

resulted in an estimate that they are of about the size of very large molecules or small aggregations of such molecules. Since both genes and viruses seem to be of about the same magnitude and both of approximately molecular dimensions, it has been suggested by recent writers that viruses may be free, independent genes. If such a suggestion be accepted, it follows that life can exist in units far below the cellular level of unity. While this may be true, it seems safer at present to avoid premature speculation, to stay on firmer ground, and to regard cells as the primary level of life units. Starting with the cell level of units we may safely proceed to consider a progressive series of units above the cell level of organization.

Unicellular Individuals, Cell Aggregates, and Multicellular Individuals.—Very large numbers of animals, plants, and bacteria exist in which the individual consists of but a single cell. Many of these creatures are highly complex in structure, but nevertheless

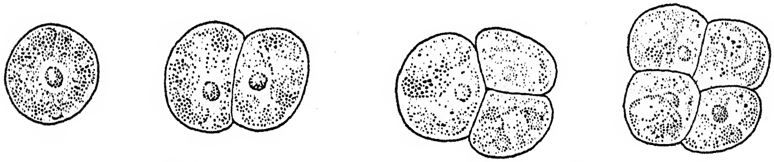


FIG. 16. *Pleurococcus vulgaris,* a unicellular green plant. Separate individual and temporary cell groups formed by cell division. (From Woodruff.)

are one-celled in the sense that they have but one nucleus. Since we shall have much to say about Protozoa (one-celled animals) in subsequent chapters, we shall for the present say no more about them.

Now throughout both the animal and plant kingdoms there is a tendency for individuals or units of the lower levels to form social groups of greater or less coherency. A study of progressive series of such aggregates brings to light a graded series of conditions between one level of unity and the next higher one.

Among unicellular plants and animals, there are many types of purely temporary aggregations of cell individuals. In *Pleurococcus* (Fig. 16), for example, a single cell divides into two daughter cells and each of the latter divides again without any separation of these cells from each other until some time later. For a certain period we have aggregates of four or more cells, which appear to be multicellular individuals but are not, for all cells are the same,

they are not interdependent, and they all become separate individuals later on. Other kinds of unicellular types form more or less stable aggregates known as COLONIES, composed of many one-celled individuals. Such colonies (Fig. 17) do not decompose as a whole into individual cells, but some cells of a special sort are released to act as REPRODUCTIVE CELLS or GERM CELLS, and from these new colonies arise. These germ cells leave the colony without destroying the integrity of the latter. Some of these colonies

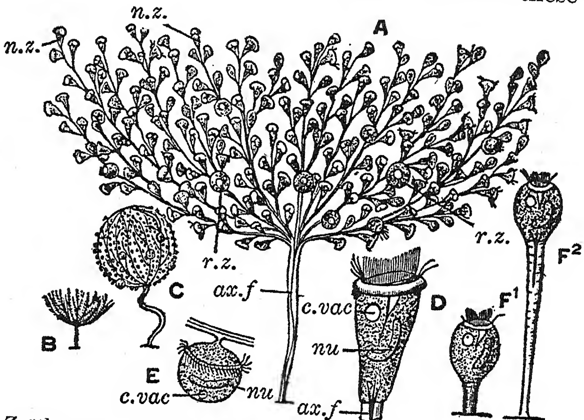


FIG. 17. *Zoöthamnium arbuscula*, a colonial ciliate protozoan. A, entire colony; B, the same, natural size; C, the same, retracted; D, nutritive zoöid; E, reproductive zoöid; F^1, F^2, development of reproductive zoöid; *ax.f*, axial fiber; *c.vac*, contractile vacuole; *nu*, nucleus; *n.z.*, nutritive zoöid; *r.z.*, reproductive zoöid. (From Parker, after Kent.)

such as *Volvox* (Fig. 18), for example, approach very close to the status of being multicellular individuals, for the various units of the spherical colony are connected by protoplasmic bridges and the locomotor activities of all the units are so coördinated that the colony swims about in such a way as to give one the impression that it is a single individual. Moreover, it is said that the unicellular individuals on one side of the sphere always go ahead in locomotion and have larger eye-spots (light sensitive organelles) than do the rest of the individuals. This would seem to imply that this region exercises a slight organizing or coördinating influence over the whole colony. If such central control could be conclusively demonstrated for Volvox, it would be difficult to deny that this form is a true multicellular organism. Even if we do not care to admit Volvox into the ranks of multicellular units, at least we can

look upon it as a very significant transitional stage between the unicellular and multicellular levels of life units. More will be said about this situation when we come to discuss the relation between

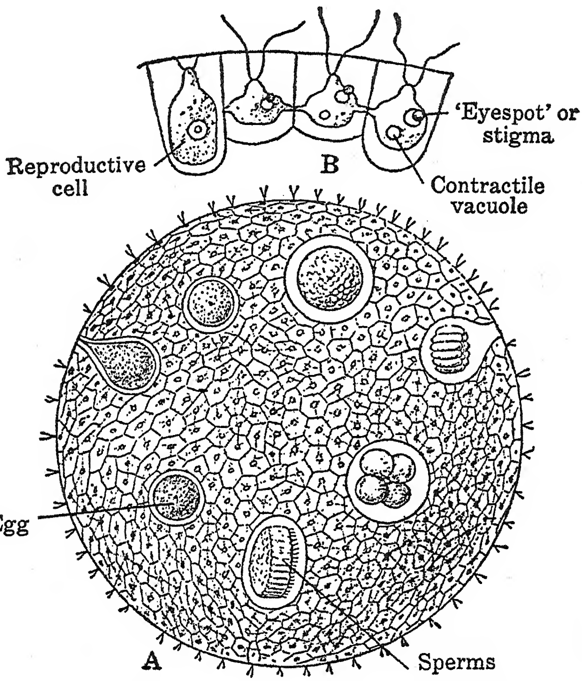
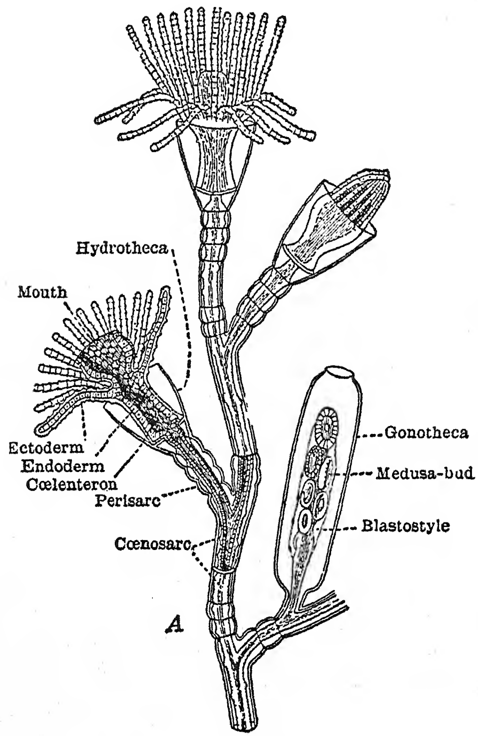


FIG. 18. *Volvox globator.* A colonial flagellate composed of hundreds of unicellular units rather closely integrated to form almost a true multicellular individual. A, a whole colony with sperms and eggs (gametes) and new colonies. B, a few nutritive cells, under higher magnification, the one on the left enlarging to form a reproductive cell. (After Woodruff.)

Protozoa and Metazoa and the probable origin of the latter (Chap. XVIII).

Multicellular Units of the First and Second Orders.—Almost exactly equivalent transitional stages are found between multicellular individuals and multi-individual units of the next higher order. Thus there are many types of multicellular animals that reproduce by budding or fission, the new individuals forming temporary colonies of units that for a time are somewhat interdependent, but which very soon break up into entirely separate individuals. Thus the common fresh-water hydra (Fig. 114) buds off one

or several new individuals that remain attached for some time to the parent individual forming a temporary colony or family. Various colonial hydroids, relatives of Hydra, show graded transitions leading toward social units of a higher order. Among the so-called colonial hydroids there are species that, from one original hydra-like individual, give rise by repeated budding to branching colonies of semi-independent individuals. These remain connected with one another by their digestive tracts so that food obtained by one may be passed to another. An example of such a colonial type is *Obelia* (Fig. 19). Here only two types of individuals are produced, hydranths and medusa buds, the latter destined to break loose and to become sexually mature individuals. An Obelia colony is a rather loosely organized social group, but it represents a step toward a complex individual of a higher order. Certain other colonial hydroids seem to us to have fully attained this higher order



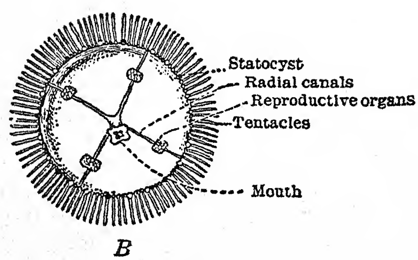


FIG. 19. *Obelia.* *A*, a small part of a large colony of hydra-like individuals, showing three nutritive and one reproductive individual (lower right). *B*, a medusa individual derived from a medusa bud of *A*. (From Parker and Haswell.)

of unity, namely the Siphonophora and the Pennatularia (commonly called, respectively, Portuguese man-of-war and sea-pens). In the Portuguese man-of-war (Fig. 20) we have a fairly closely knit society of variously modified individuals, specialized in various ways to perform functions not for themselves alone but for the whole society. One individual swells up into an immense gas-filled float, others act as food capturers and digesters, others as locomotor units, and still others as well-armed protectors. When a fish is caught, all or most of the individuals act in harmony to hold and digest it. Some biologists look upon a Portuguese man-of-war as "a single individual in which the various organs have become multiplied and dislocated." Much the same situation exists in the sea-pens, but we shall omit a description of them here. Suffice it to say that some writers claim for them that the social aggregate which they form, if not completely an individual of a higher order, closely approaches such a condition.

Another type of social aggregation that leads toward a higher order of individuality is seen among some of the flatworms, notably in *Microstomum* (Fig. 130), where the parent individual gives rise first to two individuals by dividing its wormlike body across the long axis (by transverse fission) into two nearly equal individuals. These remain attached, but the part that possessed the original head retains control. Each of the two daughter individuals divides again, resulting in a chain of four zoöids, and these four may divide again to form a chain of eight. Sooner or later they all break apart to form independent individuals like the original parent. While they are attached, however, they are dominated and controlled in their movements by the anterior piece which acts as a head. We may assume that if at some time such chains of ZOÖIDS as these came to be somewhat more forcibly dominated by the head of the original individual so that they could not become completely self-sufficient and therefore could not free themselves, the linear chain or colony might have become a single new individual of a higher order, with a segmental organization. A commonly accepted theory as to the origin of the segmented worms (Annelida), a theory known as the ZOÖID THEORY OF METAMERISM, holds that the annelids have been derived from ancestors somewhat like flatworms through such transitional forms as that represented by *Microstomum*. This would be a case in which a colony or society of multicellular individuals had evolved

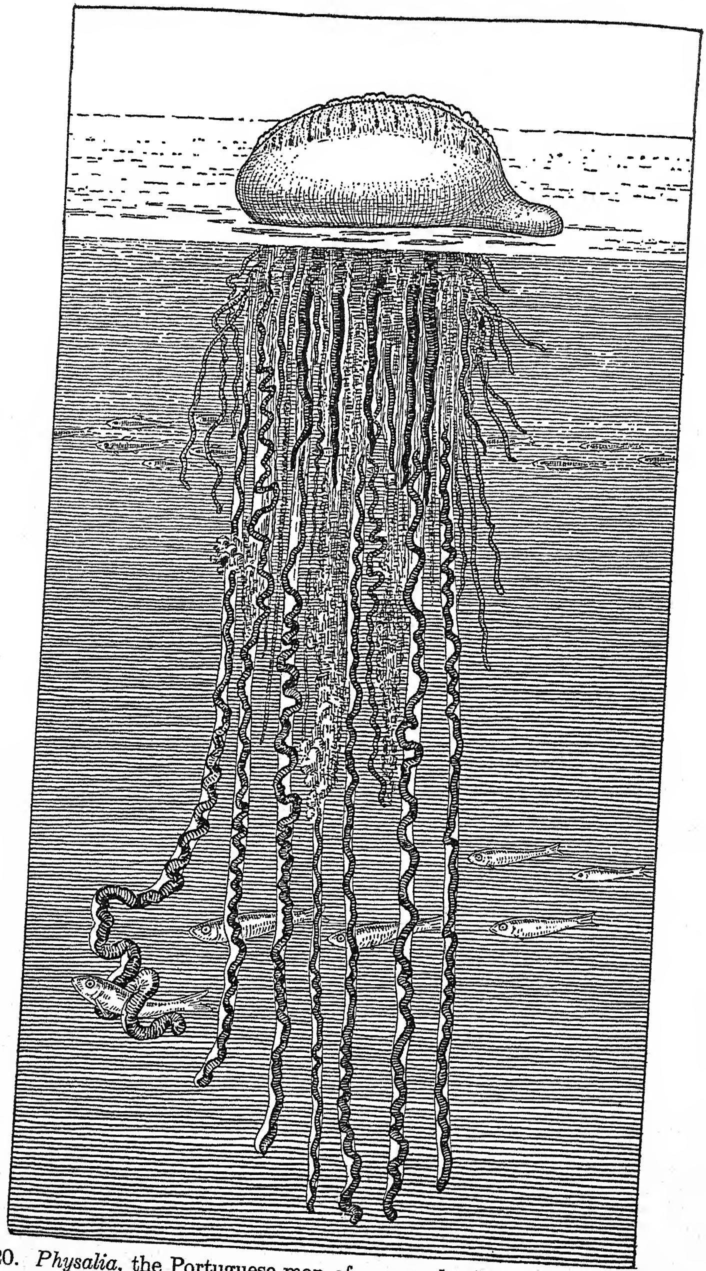


FIG. 20. *Physalia*, the Portuguese man-of-war, a closely integrated colony of hydroid individuals that closely approaches the condition of being a single individual.

into a closely knit higher type of unit, the so-called *metameric* type.

Societies of Physically Separate Individuals as Units of a Still Higher Order.—The segmental type of organism and the colonial-hydroid type of individual such as *Physalia,* may be regarded as multicellular units of a second order composed of multicellular individuals of the first order joined together physically and physiologically by material bonds. There exist, however, also many social units composed of entirely separate complex individuals integrated only by psychic bonds, which bind them more or less closely into units of the next higher order, SOCIETAL UNITS. The best examples of true societal units are found among certain groups of insects: bees, wasps, and ants (Hymenoptera) and termites (Isoptera). In these insects the social group is a true family group centering about a queen-mother, who is the center of the organization. Specialization of individuals within the unit, such as workers, soldiers, males, etc., makes one type dependent on the others and this mutual interdependence acts as a further binding force unifying the group into something very much like a true organism. So closely integrated are some of these societies that members of one society always recognize their own fellows and accept them, but will not tolerate a member of another group. Termites form societies even more elaborate than do ants, for in some species the specialization of different kinds of individuals, all progeny of the same mother, is carried further than among any of the ants.

A still further advance in social organization is also found among ants and termites. There are cases in which a single social unit is composed of individuals belonging to two distinct species, as in slave-making ants. In these social units one species of warrior ants captures the young of another species of ant. These young, growing up in the homes of their captors, do all the domestic work of the society in addition to feeding the soldiers and their progeny. The slave-making species is utterly dependent on the slave species for its continued existence and in return protects the whole complex unit from alien attack. Such a compound society seems to deserve rank as an organized unit of a higher level than any unit composed of only one species.

Far more complex even than this type of two-species society, are the multi-species aggregates found among most species of ants and termites. In almost every social unit of these animals there are

numerous uninvited "house guests" belonging to alien orders of insects. Some of these house guests are ants belonging to other species constituting a beggar or thief class, others are beetles, bugs, spiders, etc., that have assumed disguises causing them to be mistaken for ants. Such societies as these, composed of an owner species, itself consisting of several specialized castes, and sometimes a dozen or more species of house guests living upon the bounty of the hosts, constitute perhaps the most complex of closely integrated social units, even more complex biologically than human societies, and certainly more tightly integrated and much more stable. Tempting as it is to include the various levels of human social units in this series, we feel that this is scarcely the place to discuss the resemblances and differences between human and non-human social units. Such a discussion would lead us too far afield.

Ecological Complexes as Life Units.—We cannot avoid, however, some mention of what we believe to be the most elaborate of all social units, namely, the so-called *ecological complexes*. In any natural area of the world large numbers of species of animals and plants exist in a state of mutual interdependence. Any particular species constitutes one thread in an intricate "web of life," the whole ecological fabric constituting a fairly definite social unit. Any given species is part of a nutritive chain or cycle, for it feeds upon some members of the complex and is the food of others. Any serious over- or underproduction of any one species upsets the balance of the whole complex. A small pond may be taken as an example of such an organized social unit. Each of the hundreds of species of animals and plants living in or about such a pond has relations intimate or remote with all the rest. Normally, the whole complex is in a state of equilibrium with regard to the relative abundance of the various species, for there are efficient checks upon the overproduction of any single species. If, however, external factors bring about the reduction in numbers or extermination of any one species, the elaborate system of interdependencies may be seriously upset, causing changes throughout the whole. Sooner or later a new equilibrium will be attained, but the complex unit will not be the same in any respect as it originally was. Such a complex system of interdependencies as this cannot be thought of as a chaotic assemblage or miscellany of diverse living organisms: on the contrary, because there are very definite and orderly relations between its various parts, it has many features of an organ-

ism. Hence it seems legitimate to consider it as the highest even if not the most definite, of the various levels of organized life units.

In this whole discussion the social note has been dominant. It is our conviction that life is essentially a social phenomenon. Life is possible only in connection with units that are complexes of parts differing from one another in their properties, but so ordered that they have relations of mutual benefit to each other and to the whole. Such organization seems to us essentially social. The more specialized the various parts of the organism are, the greater their interdependence. The more complex the organism is, the greater the necessity for coördinating and integrating the activities of the parts. The most efficient organisms are those which are on the one hand the most complex because of their numerous specialized parts, and on the other hand the best provided with coördinating and integrating mechanisms.

Evolution from the lowest to the highest forms of life has as its chief motif increasing specialization of parts with closer integration of these parts into coherent wholes. The special mechanisms of integration, nervous and hormonal, will be discussed in a subsequent connection.

SUMMARY

1. The most important fact about life units is that the parts are organized into wholes. Organization is the keynote of life.
2. The individual is the true unit at whatever level of complexity it may be.
3. In many ways the cell is the supreme biological unit. A cell may constitute a whole individual or be a minute part of an individual.
4. There may be life units below the cellular level, namely, viruses and possibly free genes.
5. Cells aggregate to form a graded series ranging from loosely integrated units (colonies) to closely integrated units (multicellular organisms) that are regarded as units of a higher order.
6. Multicellular organisms also aggregate to form more or less closely integrated colonies. Some of these aggregations are so closely integrated as to produce units of a still higher order.
7. Social units composed of many multicellular individuals are held together by bonds of instinct, not by bodily union.
8. Animal and plant communities composed of many interdependent species constitute life units that are held together through a network of interdependencies. They constitute a "web of life."
9. At each higher level of life units new properties emerge that are characteristic only of that level and are not expressed in the parts making up the whole.

CHAPTER VI

CELLS, THE MOST FUNDAMENTAL LIFE UNITS

A. General Characteristics of Cells

As has already been said more than once, cells may be regarded as the most fundamental of life units in much the same sense that star-suns are considered the most fundamental of cosmic units and atoms the most fundamental units of matter. Cells, however, are not by any means the only important life units, for there are levels of unity both below (if viruses are units) and above the cellular level. In unicellular animals and plants the cell unit is also the whole organism, but in multicellular animals and plants the cells are only minute parts of the whole organism, and the organism as a whole dominates its parts, as will be more fully brought out in a subsequent connection. Whether a cell constitutes a whole organism or is merely one of millions of minor units integrated to form a complex organism, it is a cell by definition.

The cell has been variously defined as "the unit of structure and function in animals and plants," as "the smallest living unit capable of independent existence," as "a small mass of living matter containing a nucleus or nuclear material." The first definition fails because cells are not the only units of structure and function; the second fails because it does not take into consideration that filterable viruses seem to be living and are probably simpler than true cells; and the third fails because there are some plant cells, such as the blue-green algæ and bacteria, in which the protoplasm is not differentiated into nucleus and cytoplasm. The term "cell" is difficult to define because it represents an abstract generalization that attempts to cover too complex a field. It is possible, however, to give a general description that will cover the majority of units of the cellular level of organization and this we shall soon proceed to do, but first let us review a few facts about the size, shapes, and numbers of cells.

Dimensions of Cells.—In Chapter III we made the somewhat startling statement that life units as a whole occupy a median

position in the scale of dimensions of nature's units. Let us be somewhat specific about this matter and consider the actual size of various kinds of cells. No one knows how small the smallest cells may be, for there seem to be some bacteria that are invisible under the highest powers of the microscope. It is even suspected that at least some of the so-called viruses that pass through filters are merely bacteria of exceedingly small size. Bacteria of average size are somewhat less than one ten-thousandth of an inch in length and about half that in diameter. Thus about ten thousand of them could be placed end to end across the diameter of a half dollar. When we recall that the diameter of an atom is estimated to be 10^{-8} cm., or that approximately 3,000,000,000 atoms could be placed side by side across a half dollar, we realize that even the tiniest of cells is relatively quite large, being about 300,000 times as large in their longer diameter as an atom. Another way of visualizing the relative size of cells is that of calculating the number of cells in the human body. Cytologists tell us that there are 10^{13} blood cells in the human body, a staggeringly large number. The total number of cells in the whole body must be at least fifteen times that of the blood cells, for the blood constitutes about one fifteenth of the total body weight. Now while the vast majority of cells are of microscopic size there are many that are visible to the naked eye, indeed some that are quite large. Thus the yolk of a hen's egg is a single cell about an inch in diameter and that of an ostrich egg several times as large. Such cells, however, are huge merely because they are gorged with yolk, an inert food substance upon which the embryo feeds until hatching. A single nerve cell, though of no great mass, may have an extraordinary length, in some cases being several feet long. While there is this extreme variation in size of different kinds of cells, the cells of any given tissue of a particular organism are nearly uniform in size. The function of any particular kind of cell seems to have much to do with determining its size limits. If a cell is to function as a storehouse of nutriment for sustaining an embryo up to the time when it can be independent, it must be relatively large and massive. If a cell is to function as a sort of animated telegraph wire, connecting one remote part of an organism with another, it needs to be very much elongated. Muscle cells need to be elongated when at rest so that when they contract they may shorten up.

Lining, or epithelial, cells need to be pavement-like or tilelike, so as to form firm, smooth surfaces (Fig. 21).

While the shapes of cells are many and varied, the typical shape

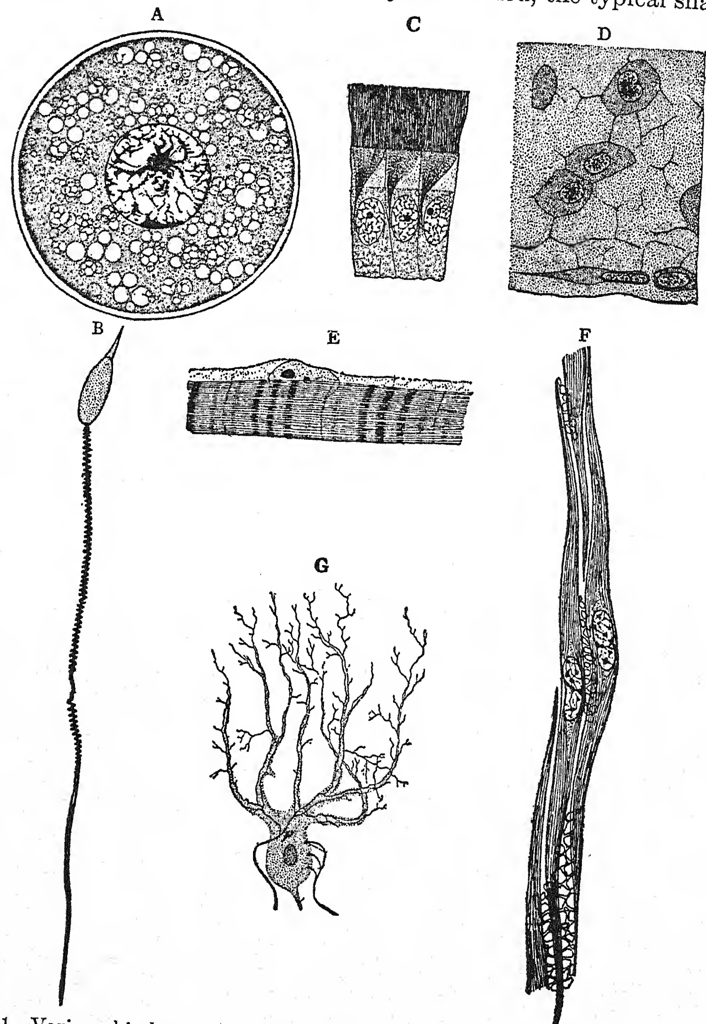


FIG. 21. Various kinds of cells. A, female germ cell, ovum of a cat. B, male germ cell, spermatozoön of a snake, *Coluber*. C, ciliated epithelium from the digestive tract of a mollusk, *Cyclas*. D, cartilage of a squid. E, striated muscle fiber from an insect larva, *Corydalis cornutus*. F, smooth muscle fibers from the bladder of a calf. G, a nerve cell from the cerebellum of man. (From Hegner after Dahlgren and Kepner.)

of a cell uninfluenced by inequalities of environment, pressures, specialized functions and relations, is spherical, because a fluid system, on account of the tension of the surface membrane, tends to assume the most compact form with the least possible surface for a given mass—the sphere. It is mainly in free cells such as eggs and in some of the Protozoa that we find the true spherical form retained. The demands of the Protozoa for locomotor organs, or for a shape with stream lines adapted to swift motion through a resistant medium, cause these active types of cells to modify their spherical form in an amazing variety of ways. Only when such cells go into a "resting" condition do they assume the typical spherical form. Many cells have a more or less stiff surface covering—pellicle or cortex—that serves to hold the body in a permanent, though flexible, shape; while other cells, such as leucocytes and amœbæ, are constantly thrusting out long fingerlike processes (pseudopodia) which serve as feet for walking and hands for grasping and mouths for engulfing food.

TISSUES are aggregates of similar cells performing similar functions. Such cells, packed close together as they are, are subject to the laws of mechanics, and just as inert units would do under similar conditions, they assume the form of polyhedrons of various types, depending on their functions and the physiological demands of the case. They may become elongated rectahedrons; they may be flat and tilelike; they may be elliptical, spindle-shaped, discoid, or stellate—each according to its surroundings and the rôle it has to play in the organism. In spite of this almost limitless variety of size and shape, however, all cells have an organization dependent upon the possession of certain components necessary for cell life.

B. THE VISIBLE STRUCTURE OF CELLS

1. *Nucleus and Cytosome*

Some of the simplest plant cells consist of merely a mass of homogeneous protoplasm, with a cell membrane but no other differentiated parts. All animal cells, however, are more complex than this. In addition to the cell body, known as the CYTOSOME, there is always a second internally placed body, known as the NUCLEUS. Both cytosome and nucleus are composed of living protoplasm, but they differ from each other both physically and chemically. We commonly speak of the cytosomic protoplasm as CYTOPLASM and of the nuclear protoplasm as NUCLEOPLASM.

Both cytosome and nucleus are commonly quite complex in structure, each composed of a number of characteristic differentiated structures. Figure 22 shows in diagrammatic fashion a sort of composite cell containing most of the types of formed components found in both plant and animal cells. No single kind of cell is possessed of all the structures shown in this illustration.

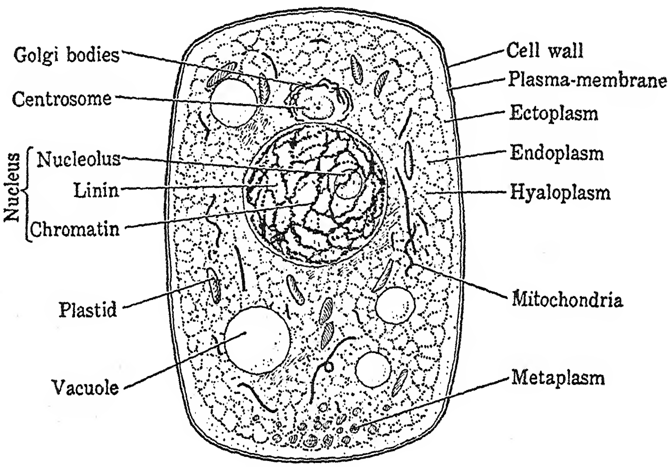


Fig. 22. General diagram of a cell. (From Woodruff after Wilson.)

Since cytosome and nucleus are the two primary parts of a cell, all other details of cell structure may be described as formed components of one or the other. We shall first describe the formed components of the cytosome and then those of the nucleus.

2. *The Formed Components of the Cytosome*

The variety of formed components of the cytosome is so great that in this brief survey it is necessary to confine attention to a few of those whose occurrence is most general. Following ***Professor E. B. Wilson,*** we may consider these as belonging to eight categories:—central bodies, cytoplasmic granules, fibrillæ, plastids, chondriosomes, Golgi-bodies, vacuoles, and cell membrane.

a. Central Bodies.—The term central body (also centrosphere) is applied to that structure which lies at the focus of the astral rays during mitotic cell division. It is usually rather small and relatively inactive during the so-called resting, or vegetative, phases of cell life, but awakens to intense activity during the ac-

tively dividing phases. In the resting state the central body consists typically of a sphere of more or less hyaline protoplasm in the center of which lies a minute granule, or more commonly a twin pair of these, known as the CENTRIOLE (also called centrosome). While the central body usually lies close to the nucleus it may be either considerably removed from it or else be located within the nucleus. In the chapter on cell division the central body will receive further attention.

b. Cytoplasmic Granules.—There is a confusing array of many different sorts of granular cytoplasmic components all suspended in the clear, hyaline ground substance, or HYALOPLASM. In size these granules range from those so small as to be nearly at the extreme limit of microscopic visibility to those of relatively large size, such as yolk granules. A rather complicated terminology has been devised to aid in the classification of cytoplasmic granules, but it must suffice here to mention only a few of the main types, such as microsomes, chondriosomes, secretory, storage, and pigment granules.

c. Fibrillæ.—These are among the most striking and significant of cytoplasmic structures. Muscle fibrillæ, or myofibrils, have a precise and characteristic arrangement and appearance and are doubtless responsible for muscular contractility. In nerve cells there is usually a definite network or basketwork of fibrillæ, neurofibrils, that come together at one pole of the cell and pass out into the cell process, or axis-cylinder. Many types of gland cells and certain kinds of epithelial cells also possess conspicuous fibrillar components.

d. Plastids.—These are far more common in plant cells but are found also in a few types of animal cells, notably in some flagellate protozoa. Among plants the most important type of plastid is the chloroplast, the green body that gives color to leaves and other structures and that is responsible for the synthesis of starch out of the raw materials, water and carbon dioxide.

e. Chondriosomes.—These bodies occur in nearly all kinds of cells. Usually they are granular, rodlike, or filamentous in form at any given moment, but in living cells they appear to be constantly changing position and form. These most plastic of all cell components are believed by some cytologists to be formative bodies out of which the various other, more stable, cell structures, such as plastids, fibrils, and various specific types of granules, are produced.

f. Golgi-Bodies.—These elements are quite distinct both morphologically and physiologically from chondriosomes, though they are sometimes confused with them. They occur in two main forms, localized and diffuse. When differentially stained, they appear as loops or networks occupying definite positions. Very little is known as to their function.

g. Vacuoles.—These are spherical cavities filled with fluid substances of various kinds, each bounded by a delicate film. Under this head come various types of cell organs to be studied later, such as the food vacuoles and contractile vacuoles of Amœba and Paramecium. In some cells the vacuoles are so conspicuous that the whole cytoplasm has a foamy, or alveolar, appearance. Vacuoles are especially prominent in plant cells and in the Protozoa among animals, but are not usually well developed in the cells of higher animals.

h. Cell Membrane.—All cells, even those apparently naked cells such as Amœba and leucocytes, have at least a PLASMA MEMBRANE, or limiting surface membrane. This is considered as the true cell membrane and must not be confused with the cell wall which lies outside the cytosome, sometimes separated from it by a considerable space. The CELL WALL is usually regarded as a protoplasmic product and is not believed to be truly living even though in some cases it seems to be capable of growth.

The plasma membrane is the surface film of the cytosome, comparable with the film that forms at the surface of certain colloidal systems such as that on the surface of scalded milk. This membrane possesses considerable toughness and elasticity and serves to protect the cytosome from dissolution and from chemical and mechanical injury, while at the same time it is sensitive and responds readily to stimuli by changes of form and permeability. It has the capacity of SEMIPERMEABILITY, permitting the passage of solvents and some solutions while preventing the passage of colloidal materials and of other substances in solution. This property is of the utmost importance in the life of the cell, in as much as protoplasm is essentially a colloidal system that would readily be disrupted were it not protected from coming into direct contact with water and other materials in the surrounding medium. Yet it is imperative that various substances involved in the metabolic activity of the cell should have free ingress or egress through the cell membrane. No more important structure of cells exists

than the plasma membrane, for it is responsible for maintaining the individuality of the cell and presides over the chemical traffic of the protoplasm that constitutes the essence of its life.

3. *Components of the Nucleus*

While the typical form of nuclei is spherical or nearly so, there are many other forms. Some are horseshoe-shaped, others resemble chains of beads, still others are more or less branching or even reticular. In some cells, notably the bacteria, the nuclear material is diffusely scattered throughout the cytoplasm in the form of numerous granules. In other cells there may be two or several nuclei. Whatever the form of the more massive types of nuclei, all are more or less complex in organization and, as in the cytosome, there are several well-defined categories of components, among which the following are nearly universal:—nuclear membrane, nuclear framework, nucleoli, and nuclear sap.

a. Nuclear Membrane.—This delicate but well-defined surface film plays the rôle of arbiter over the chemical exchanges between the nucleus and the cytosome and, like the plasma membrane, is semipermeable. Microdissection has demonstrated that it possesses considerable toughness and elasticity. At times however, especially during mitotic cell division, the nuclear membrane breaks down and the nucleoplasm and cytoplasm become very intimately commingled. After mitosis the membrane is reconstituted. In some cases this membrane seems to be formed exclusively of nuclear material; in other cases it is formed partly from the cytoplasm.

b. Nuclear Framework.—This part of the nucleus contains the most distinctively nuclear materials, for it is made up of a complex spongy network of CHROMATIN (basichromatin) and LININ (oxychromatin). The exact interrelationship existing between these two materials is not yet fully clear. It is sometimes difficult to distinguish sharply between them. In the growing, or vegetative, phases of cell life, the chromatin proper appears to exist in the form of numerous granules of varying sizes strung upon a linin network. When, in division stages, chromosomes are formed, both chromatin and linin contribute to their substance. In several later chapters chromosomes will receive much attention on account of the fact that these bodies play a very important rôle in heredity.

c. Nucleoli.—This term has been applied to quite a variety of entirely different nuclear bodies and some confusion exists as to

just what sorts of structures should be called nucleoli. It seems well to include under this head the so-called true nucleoli, or PLASMOSOMES, and chromatin nucleoli, or KARYOSOMES. The plasmosomes are entirely distinct from chromosomes, but karyosomes may be identical with chromosomes, sometimes being merely chromosomes that in the resting phases of cell division remain in a condensed state. Both kinds of nucleoli may be present at once in the same cell, but they are readily distinguishable by their different staining reactions. While the function of the karyosomes seems quite clear, since they are chromosomal in character, that of the plasmosomes is still quite problematical. There is some evidence, however, that these bodies may have something to do with the secretory processes of the cell.

d. Nuclear Sap.—While it has been generally supposed that the nuclear sap is no more than a structureless fluid, there are observations indicating that it may have a firmer consistency than that of an ordinary watery solution. The actual character of the nuclear sap is very imperfectly understood and needs investigation.

4. *Cellular Polarity*

Enough has been written to emphasize the fact that the cell, though in most cases small in size, is far from simple in its organization. No two kinds of cells are alike in their constitution, some possessing one complex of cytoplasmic and nuclear components, others another complex. Within a single organism the nuclei of all cells may be essentially alike, but there is an almost endless variety of differences in the organization of the cytosome in different kinds of tissue cells. In any one kind of tissue cell, however, the cytoplasmic constitution is fairly uniform. There is nothing indefinite about the constitution of cells, whether relatively simple or relatively complex. Each cell is a definite life unit, with a precise arrangement and interrelation of all components, large or small. A cell is a true microcosm in which innumerable minor units are ordered in all their changes so that unity and harmony prevails. This ordered arrangement of parts within the cell has been long noted by biologists and has been described in terms of polarity and symmetry.

A typical cell, such as an egg cell, has one pole at which the protoplasm is most active, where the rate of metabolism is highest, and an opposite pole where the metabolic activity is lowest. The

more active pole is usually called the ANIMAL POLE and the less active pole, the VEGETAL POLE. Between the two poles there is a gradient of metabolic activity extending down the axis. The cell is then an organized metabolic system. Besides the polarity of the cell there is to be recognized another gradient from the center to the surface. A resultant of these two gradients determines the differentiations at the various levels of the cell. As this gradient conception is to be more fully explained in a subsequent chapter we need not elaborate it further in this place.

C. The Problem of the Ultimate Physical Structure of the Cytoplasm

One of the very interesting chapters in the history of zoölogical progress centers about the attempt of both earlier and later workers to discover the essential or ultimate physical make-up of the living substance, especially of that part of it situated in the more homogeneous regions of the cytoplasm. The earlier workers attacked this problem somewhat naïvely, with the hopeful idea before them that if they could discover the construction of the machine, they would soon be led to an understanding of how the machine works, and would then be in a position to solve the perplexing problem: what is life? These hopes have been realized only very partially. As microscopic technique has been improved and refinement after refinement has been added to the optical equipment of the students of cell structure, more and more accurate pictures of protoplasmic structure have come to view. Various theories have followed one another as to the finer structure of the protoplasm:—

a. The Granular Theory.—According to the granular theory the protoplasmic mass is made up of tiny units or granules that are sometimes massed into solids and sometimes arranged in linear series so as to form fibrils.

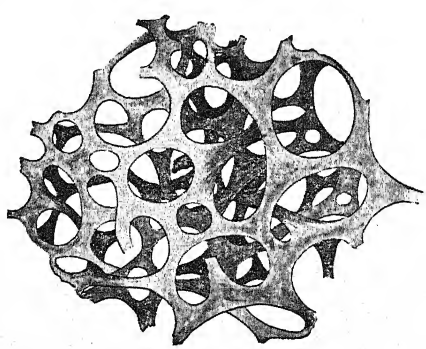


FIG. 23. Diagram to illustrate the *reticular* theory of protoplasm. (From Dahlgren and Kepner.)

b. The Fibrillar Theory.—Emphasis is here laid upon

the fibrous nature of cytoplasm, looking upon the mass as a more or less dense feltwork of fibers.

c. The Reticular Theory.—This theory emphasizes the fibrous make-up, but adds the conception that the fibers are knotted together into an intimate network like a series of hammocks knotted together, one on top of another (Fig. 23).

d. The Alveolar Theory.—The granules and fibers of the earlier theories are viewed in the alveolar theory as artifacts—appearances caused by the rough handling of protoplasm by chemical agents in process of fixation. According to ***Bütschli,*** the leading advocate of the alveolar view, protoplasm is a sort of foamy emulsion of two substances intimately mixed, much like an emulsion of oil and water. In the latter case we have fine spheres of oil in a matrix of water, each oil droplet surrounded by a film of water. In protoplasm it appears that there is a sort of ground substance, probably colloidal in character, with spheres of more liquid material suspended in it (Fig. 24). Living protoplasm, when seen free from the cell, often has the alveolar appearance, but this is only the gross, not the finer, structural organization.

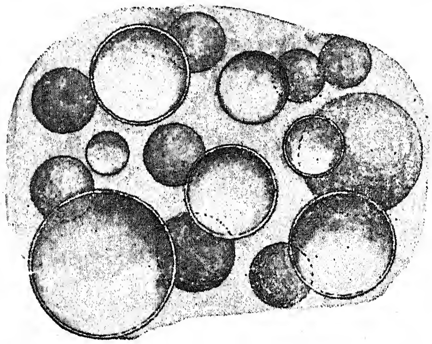


FIG. 24. Diagram to illustrate the *alveolar* theory of protoplasm. (From Dahlgren and Kepner.)

e. The Colloidal Theory.—***Professor E. B. Wilson*** has recently stated that the "so-called 'alveolar' structure is not a primary characteristic of this protoplasm. It is of secondary origin, arising by the appearance in the homogeneous ground substance of extremely minute scattered bodies which by growth and crowding together finally produce the emulsion-like structure. In the middle stages of this process the protoplasm gives an interesting picture. When viewed under relatively low magnification, e.g., 300–500 diameters, only the larger bodies are seen; but as step by step we increase the magnification, step by step we see smaller and smaller bodies coming into view, at every stage graduating down to the limits of vision. This remains true even with the highest available

powers. The microscopical picture offered by such protoplasm is thus somewhat like the telescopic picture of the sky. At each step in the improvement of the telescope new and fainter stars come into view. At each step the astronomer has felt sure that still more powerful telescopes would bring into view stars hitherto unseen. The cytologist is equally sure that if the present limits of direct microscopical vision could be extended, we should see disperse bodies still more minute; . . . below the horizon of our present high power microscopes there exists an invisible realm, peopled by a multitude of dispersed particles, a realm quite as complex as the visible one with which the cytologist is directly occupied."

We have reason to believe that the ultimate particles suspended in the aqueous matrix are masses somewhat larger than molecular size, consisting of aggregates of molecules, sometimes not very large in numbers. At this point, as Professor Wilson remarks, "we have reached the borderland where the cytologist and the colloidal chemist are almost within hailing distance of each other."

Conclusion.—We may well conclude this chapter with an important summary of his own conclusions, taken from an earlier paper by Professor Wilson:—

"My own long-continued studies on various forms of protoplasms have likewise led to the conclusion that no universal formula for protoplasmic structure can be given. . . . It is impossible to resist the evidence that fibular and granular as well as alveolar structure are of wide occurrence; and while each may be characteristic of certain kinds of cells or of certain physiological conditions, none is common to all forms of protoplasm. If this position be well grounded, we must admit that the attempt to find in visible protoplasmic structure any adequate insight into the fundamental modes of physiological activity has thus far proved fruitless. We must rather seek the source of these activities in the ultramicroscopical organization, accepting the probability that apparently homogeneous protoplasm is a complex mixture of substances which may assume various forms of visible structure according to its modes of activity."

Thus we are once more disappointed in our attempts to solve the puzzle as to the nature of life. The study of protoplasmic structure, even when carried as far as our best optical equipment permits, falls far short of revealing to our eyes the life-machine at work.

In this chapter we have gone as far as seems advisable in our attempt to describe the visible structural organization of the cell. In subsequent chapters we shall go beneath the visible features of organization and discuss the physical and chemical organization of cell units.

SUMMARY

1. The cell, when regarded as the unit of structure and function in organisms, is examined in some detail in this chapter.
2. Cells vary in size, some being millions of times larger than others.
3. The total number of cells in the human body has been estimated as being about 1,500,000,000,000,000, a staggering figure.
4. The shape and size of cells varies with their function in the organism.
5. The visible organization of the cell as revealed by the microscope consists of nucleus, cytoplasm, and both nuclear and plasma membranes.
6. The formed components of the cytosome are: central bodies, granules, fibrillæ, plastids, chondriosomes, golgi-bodies, vacuoles, and cell (plasma) membrane.
7. The plasma membrane has the property of semipermeability and thus regulates the energy traffic of the cell.
8. The components of the nucleus are: chromatin, linin, nuclear sap, nucleoli, and nuclear membrane.
9. Most cells are organized along lines of polarity, with an animal and a vegetal pole and one or more metabolic gradients.
10. Various theories of the ultimate finer structure of the cytoplasm are discussed, no one of which seems adequate. The view that the cytoplasm is an intricate colloidal system involving many kinds of components is doubtless most acceptable.

CHAPTER VII

THE CHEMICAL AND PHYSICAL CONSTITUTION OF LIVING MATTER

A. Matter and Energy

We have considered so far chiefly the visible organization of the cell. The laborious effort to solve the mystery of life through the elaborate technique of microscopy has left us confronted with a stubborn unsolved problem: what is the nature of life? We cannot solve this problem at the levels of visibility. Perhaps the secret lies in the invisible physical and chemical constitution of living matter.

Let us now examine the chemical ingredients and physical properties of the substances that make up living units. But first of all let us say a few words about matter and energy in general so that we may have a better appreciation of the peculiar expressions of matter and energy found in organisms.

Science today holds that all the realities of the physical world are expressions of two fundamental entities—matter and energy. Matter is defined as something that occupies space, has mass (inertia) and weight. All material things, living and lifeless, are composed of matter. Matter, however, is always in action to a greater or less extent. The activities of matter are the result of energy changes. Energy is defined as "the capacity to do work, the ability to produce movement and change in matter." Everything that happens in nature, even in living beings, is supposed to be due to changes in the relations of material substances and to energy changes or transformations.

The Units of Matter.—In Chapter III we have already introduced you to atoms, electrons, etc., when dealing with nature's scale of dimensions. Now we shall study the activities of these units. All material things are made up of minute discrete particles called molecules, the smallest units into which a substance can be divided without destroying its identity. The number of different kinds of molecules is almost unlimited, for there are as many kinds as there are pure substances.

The molecule, however, is not the smallest unit of matter, for all molecules are composed of lesser particles, called ATOMS. Only 92 different kinds of atoms are known. Each kind of molecule consists of a definite kind and number of atoms combined in a definite way. Some molecules consist of only two atoms, others of hundreds of atoms. The simplest molecules consist of combinations of two atoms of the same kind, as when two atoms of hydrogen combine to form a molecule of hydrogen, H_2. All chemical actions are the result of breaking down molecules and combining their constituents in new ways. Such changes either take up energy or release energy.

Even atoms are not ultimate units, for every atom is composed of excessively minute particles of which there are two main kinds, PROTONS and ELECTRONS. (For present purposes we shall leave out of consideration neutrons and other units recently discovered.) Protons and electrons are particles of electricity, protons being positive and electrons negative in charge. Each kind of atom has a definite number of protons and electrons organized into a definite system. Thus organization here as well as in living units lends character to each kind of unit and confers upon it its peculiar properties. Even at this level there are properties of the whole which are not merely the sum of those of the parts.

Any kind of substance which contains equal numbers of protons and electrons is electrically neutral, for each positive charge is neutralized by a negative charge. Many substances, however, have unequal numbers of protons and electrons and therefore carry excess charges on the surface of either positive or negative electricity. Substances with like charge repel each other, but those with opposite charge attract. Two kinds of substances with opposite charges tend to be brought together to form new compounds. This is the nature of chemical reaction.

All whole atoms and molecules are electrically neutral but many of them break up under certain conditions, especially when dissolved in water, into smaller particles called IONS, which are positively or negatively charged. The reason why chemical changes take place more readily when substances are dissolved in water is that neutral molecules are broken up into charged ions that tend to reunite in new ways. We speak of substances capable of breaking up into ions when in solution as ELECTROLYTES. Much of the activity that goes on in living matter is due to the fact that the

latter is composed so largely of water and that, therefore, there is opportunity for ions to react with one another.

Different Kinds of Energy.—Energy expresses itself in many ways. Energy is used in all movements of larger and smaller bodies. It may express itself as heat, electric currents, light, or other radiant forms. It is involved in all chemical changes. All energy changes consist of movements of matter of one kind or another. Heat is the result of movements of molecules, chemical change of atoms, and electrical currents of electrons. Energy may be either POTENTIAL or KINETIC. Thus a heavy weight on a table has potential energy which is expressed as kinetic energy as it falls from the table to the floor through the force of gravitation. Gunpowder has a lot of potential energy that is released as kinetic energy when it explodes. Kinetic energy is the energy of movement whether it be in a falling body or in an explosion. The various manifestations of energy are capable of being transformed the one into the other. Thus heat energy may be transformed into motion, into electric current, or, in living organisms, into growth and reproduction. Energy is never lost: it is merely changed from one form into another. This fact is embodied in the LAW OF THE CONSERVATION OF ENERGY. All other forms of energy tend to be transformed into heat, the end product of energy expressions. This one-directional tendency of energy transformations is expressed in the second law of thermodynamics, the LAW OF ENTROPY.

With this brief outline of a few of the main principles of physical science before us, let us attempt to apply these principles in an effort to understand the physical and chemical constitution of living matter and the peculiar energy transformations that are carried on in living cells. But first of all it seems necessary for us to speak briefly about protoplasm, the name commonly applied to the material substances found in living units.

B. The Protoplasm Concept

Throughout this account of the physical and chemical characteristics of cells we shall use here and there the term "protoplasm." The term is a convenient one and has been variously defined as "living matter," "living substance," and "the physical basis of life." It is a mistake, however, to look upon the materials out of which living units are made as being alive, for only the complete life unit is alive. None of its parts is of itself alive. It is

equally a mistake to use the term protoplasm in any sense implying that there is but one such substance common to all kinds of living cells. The structure and composition of different kinds of cells vary tremendously and yet the active materials of all of them equally deserve to be called protoplasm. If we were to use the term protoplasm at all we must use it merely as a convenient substitute for the phrase "complex colloidal system constituting the active part of cells, with all its proteins, lipins, carbohydrates, enzymes, salts and water." There is no one protoplasm: on the contrary, there are as many protoplasms as there are different kinds of life units. The term protoplasm is merely a convenient abstraction and we should use it cautiously with this in mind.

C. The Chemical Constitution of Living Matter

1. *The Kinds of Elements in Living Matter*

One fact about the chemical composition of living matter stands out prominently: there is no unique life element in it and the elements that make up its compounds are relatively few and of the most ordinary and abundant sorts found in the world. These few elements are all abundant and widely distributed and the necessary ingredients for living matter can be gathered at almost any spot on the globe. The elements found in protoplasm are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, chlorine, sodium, potassium, calcium, magnesium, iron, iodine, and sometimes silicon, copper, and a few others.

The chemical elements in the human body, for example, are found to exist in about the following percentages by weight:

Oxygen (O)	65.08%
Carbon (C)	18.00
Hydrogen (H)	10.00
Nitrogen (N)	3.00
Calcium (Ca)	2.00
Phosphorus (P)	1.00
Potassium (K)	0.35
Sulphur (S)	0.25
Sodium (Na)	0.15
Chlorine (Cl)	0.15
Magnesium (Mg)	0.05
Iron (Fe)	0.004
Iodine (I)	traces

A useful memorizing scheme, suggested by a colleague, may be made out of the chemical symbols as follows: "C HOPKINS

CaFe Mg NaCl." This may be read as "C. Hopkins' Cafe, mighty good (Mg) if taken with a grain of salt (NaCl)." This sounds silly but has helped many students. There is, as we have said, nothing peculiar or startling about this array of elements, for all of them are among the commonest on earth. More striking is the fact that 96 per cent of the whole body is composed of only four very common elements, oxygen, carbon, hydrogen, and nitrogen. Of these, carbon is the most significant, for this element has chemical properties of a special sort that favor the formation of the large, complex molecules so abundant in living matter.

Now that we have discovered the atomic composition of living matter we see nothing in it to account for life. An attempt to understand the nature of living units by analyzing them into their atomic ingredients is almost as futile as an attempt to understand a cathedral in terms of the bricks, stones, wood, glass, and mortar that were used in building it. In one case as in the other we may rest assured that the true character of the complex unit inheres in the organization of materials, not in the materials themselves.

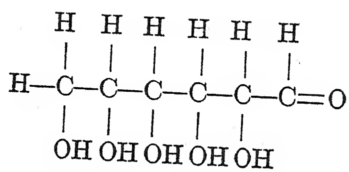
2. *The Molecular Composition of Living Matter*

While an analysis of the elements found in living matter gives us no clue to the nature of life, we get some light on our problem from a study of the kinds of molecules (compounds) present. Now it happens that there are four kinds of substances always present in living matter that are never found naturally in lifeless matter. Some of these have been completely synthesized in our laboratories, others have been partly synthesized and still others, the most complex ones, have as yet baffled all attempts at synthesis. These characteristic substances are carbohydrates, lipins (fat-like substances), proteins, and enzymes.

Carbohydrates.—We shall begin with carbohydrates because both their structure and their rôle in living matter are simpler than the other three substances mentioned. Common carbohydrates are sugars and starches. Although carbohydrates are actually built into the structure of some parts of the cell and also play an important rôle as part of the environment of cells, their chief function is that of furnishing a most available immediate source of energy, for they serve as fuel to supply the ever-burning "fires" of life. In more technical language, carbohydrates furnish the chief material for RESPIRATION or combustion within the cells.

When combined with oxygen, carbohydrates burn to form carbon dioxide (CO_2) and water (H_2O), and in this process latent or potential energy is converted into heat, motion, growth, or any other type of energy that may be needed in a particular cell. Thus carbohydrates may be looked upon chiefly as fuel for current consumption. But certain forms of carbohydrates such as starch in plants and glycogen in animals are stored in inert form in certain cells and constitute a reserve fuel supply for emergency uses.

In general, carbohydrates are made up exclusively of carbon, hydrogen, and oxygen, with a certain definite proportionality of these three elements: carbon and oxygen vary in relative proportions, but there are always twice as many hydrogen as oxygen atoms. The hydrogen and oxygen are therefore always in the proportion found in water (H_2O). Hence in a sense these substances may be thought of as various forms of carbonated water. Grape sugar (GLUCOSE) is the simplest sugar and has the formula $C_6H_{12}O_6$. The chemical structure of a glucose molecule is as follows:



When a molecule of glucose is fully oxidized or combusted it forms six molecules of water (H_2O) and six molecules of carbon dioxide (CO_2). In this process the potential energy stored in the molecule is released as kinetic energy.

A number of other simple sugars are known, but by far the most important of the simple sugars is glucose. Slightly complex sugars are formed by the union of two molecules of a simple sugar with the loss of a molecule of water. Thus our common cane sugar is a double sugar whose molecule is the result of combining two glucose molecules. Multiple sugars are made up in the same way out of several molecules of simple sugar. STARCHES of various plants are something like multiple sugars but consist of still larger numbers of sugar molecules. GLYCOGEN in animal tissues is so much like starch in character that it is sometimes known as animal starch. Both starches and glycogen play an important rôle in the economy of the cell, that of food storage. Both are

highly concentrated energy containing substances quite inert as such, but readily broken down by enzymes into simple sugar molecules when the system needs immediate fuel. Most of our carbohydrate supply comes to us in the form of starches or complex sugars. Before these can be taken into the blood stream, however, and carried to the ultimate consumers, the cells, they must be split up into their building stones, the simple sugar molecules. The process of splitting up these materials is carried on by enzymes and is part of the process of food digestion. One of the most complex and inert carbohydrates is cellulose, the substance of which wood is made. This substance cannot be digested by ordinary animals but there are a few animals, notably certain protozoa living in the intestines of termites, that have the ability to break up wood molecules into smaller molecules that are digestible for termites.

We have seen that carbohydrates play three rôles in cells: *a*, they furnish the most readily available fuel; *b*, they are important articles of food storage; *c*, they have a minor rôle in furnishing part of the structural material or at least are part of the essential environment of living cells.

Lipins.—These substances are sometimes known as fats, oils, or lipoids. They have a double rôle in cell life: that of entering into the structure of the cell and that of food storage. As structural components they are particularly important as materials in cell membranes, which are believed to be mosaics of protein and lipin particles with small pores between the spherical particles. As food storage agents they play the important rôle of reservoirs of concentrated food for emergency use, not for ordinary or immediate use. Lipins are found abundantly in the form of droplets scattered through the protoplasm, acting as reserve food packages. These fatty substances are excellently adapted for food storage purposes, since a given weight of fat contains more potential energy than any other kind of foodstuff. The reason for this is that, although fats contain only carbon, oxygen, and hydrogen, as do carbohydrates, there is much more carbon and hydrogen and less oxygen. This permits them to combine with more oxygen and thus to release more energy. Fats are compounds of different acids (fatty acids) and glycerol (commonly called glycerin). Some examples of fats are butter, oils from plants, and animal fats and oils.

Proteins.—While proteins are occasionally stored in bulk in seeds and in that case serve as reserve growth material for young plants, the primary rôle of these substances is that of structural material. Most of the organized structures of living cells are composed largely of proteins of different sorts. Proteins differ in their composition from carbohydrates and lipins in that, in addition to carbon, hydrogen, and oxygen, they always contain NITROGEN, and sometimes sulphur and phosphorus. Protein molecules are built up out of simpler "building stones" called AMINO-ACIDS, just as complex carbohydrates are built up by the chemical union of molecules of simple sugars. About thirty different amino-acids are known and these different building stones can be combined in almost any order and in varying numbers to form a vast array of different proteins. One of the best known proteins, HÆMOGLOBIN, the red substance in blood, has a molecular weight of 70,000, and since the average molecular weight of amino-acid molecules is about 150 to 200, there must be about 400 amino-acid molecules in each molecule of hæmoglobin. When one remembers the almost infinite possibility of forming different words from the twenty-six letters of the alphabet, he will realize what a limitless number of proteins may result from combinations of thirty different amino-acids. Every different species of animal or plant has its own peculiar proteins and it is probably largely due to this high specificity of proteins that species differ from one another as they do. Even individuals of the same species differ slightly from one another in their proteins.

Plants are able to manufacture their own proteins from carbohydrates and nitrogen derived from nitrogen-containing soil salts, but animals have to secure their proteins ready made as food materials derived from plants or herbivorous animals. The process of digestion of proteins consists of splitting up the proteins into separate amino-acids, which are small enough to pass through membranes into the protoplasm of cells. There the building stones are recombined by the aid of enzymes into the particular proteins characteristic of the species.

Enzymes.—Possibly no more important substances exist in protoplasm than the enzymes, yet we know less about their composition than about any other components of protoplasm. The most we can say about them is that they are more like proteins than anything else. Enzymes are found not only in cells but are

secreted by cells into the blood and into the digestive tract, where they act as CATALYZERS, facilitating and speeding up various special chemical changes. Each enzyme is specific for a particular kind of chemical reaction. Most of the chemical reactions that go on so smoothly and easily in our bodies can either not be duplicated at all or else only with great difficulty in the laboratory. Hence we may look upon the enzymes as key mechanisms that make life processes what they are. They have, therefore, been called "life catalysts," for they control the flow and direction of energy changes in living matter. Enzymes of different organisms differ and are specific in their actions, but enzymes of one species will often serve to facilitate reactions in another species. Hence the specificity of enzymes is not so marked as that of proteins.

Other Substances in Protoplasm.—While the substances just discussed are largely peculiar to protoplasm, there are always present many very common substances, the chief of which are WATER and INORGANIC SALTS. Strangely enough, active protoplasm is made up largely of water, the most abundant of all substances on the earth's surface. All of the other substances of protoplasm are more or less intimately bound up with water. Thus the proteins and lipins are in various states of colloidal suspension in water, while some of the carbohydrates and all salts are in true aqueous solution. The relative amounts of water in relation to the other materials vary in different species, in different cells, and at different ages. Thus young cells contain more water than old cells, and young individuals than old individuals. The following table gives the approximate percentages by weight of the various chemical ingredients averaged for a variety of kinds of protoplasm:

	PER CENT
Water	80
Inorganic Salts	1
Proteins	15
Lipins	3
Carbohydrates and other substances	1

The INORGANIC SALTS, because of the fact that they are electrolytes, split up when in aqueous solution into charged ions, which are able to combine with all the other substances in protoplasm and thereby keep up an active traffic of energy. The proportionality of the various salts of sodium, potassium, calcium, magnesium, etc., must be kept approximately constant. Interestingly

enough, the proportions of the various salts in the blood and other body fluids of both aquatic and land animals is about the same as in sea water, but in terrestrial and fresh-water animals the solution is more dilute. Excess of any one salt is injurious to protoplasm. The different ions have a sort of regulative action one upon the other so that the toxic effect of any given ion is neutralized. The study of the rôle of salts in protoplasm is one of the most complex branches of chemistry and must not be pursued further here.

From the chemical standpoint alone living matter may be considered by far the most complex of all substances or mixtures. Even the enzymes and proteins themselves are more complex than any other compounds known. Their complexity is so great as to baffle the efforts of chemists to synthesize them in the laboratory, although some of the simpler amino-acids have been made artificially. In view of the immense chemical complexity of protoplasm it should not cause surprise that the chemistry of life processes is still incompletely understood: rather, we should be surprised that so much has already been discovered.

D. The Physical Properties of Protoplasm

The keynote of the physical character of protoplasm is struck when we state that living matter exists in the form of AN INTRICATE, ORGANIZED COLLOIDAL SYSTEM. But this statement requires a good deal of explanation.

Protoplasm is a sort of liquid composed largely of water, as we have seen. Any substance composed so largely of water would be expected to have a fluid consistency. Its fluidity varies greatly in different cells and in the various parts of the same cell. Even the same part of a given cell may change in fluidity from one time to another, the changes in fluidity in many cases being almost instantaneous, as when a muscle contracts. Now these changes from more fluid to less fluid states of parts of the protoplasm depend on the characteristic physical properties of the COLLOIDS present.

Two kinds of substances are distinguished on the basis of the ways in which they combine with or dissolve in water (or other liquids): CRYSTALLOIDS and COLLOIDS. Crystalloids break up in water into separate molecules or even into ions, while colloids remain in the form of relatively large particles composed of many

or a few large molecules. When a substance breaks up completely the molecules or ions become evenly distributed in the water and are said to be in a state of true solution; but when aggregates of large molecules float about in water, as in colloids, they are said to be in a state of COLLOIDAL SUSPENSION OR SOLUTION. Now colloidal particles when widely separated from one another move about freely and do not seriously interfere with the fluidity of the suspension, but when they are closely packed together or unite in chains or networks, they tie up the suspension and make it less fluid or even practically solid. When a colloidal suspension passes from a less to a more closely aggregated state of its particles, naturally the colloidal mass shrinks or contracts and can therefore pull against resistance, or do mechanical work. Most mechanical movements in organisms are due to the contractility of colloidal substances in cells. This is especially true of muscle cells.

Two main phases of colloidal suspension are distinguished: the SOL state in which the colloidal particles are dispersed in the fluid medium and the whole system is relatively fluid, and the GEL state in which the particles form a more or less continuous network with one another, giving the whole a jelly-like or somewhat solid consistency. A good example of a colloidal sol is the white of a raw egg and of a colloidal gel the white of a hard boiled egg. In this case heat favors the change from sol to gel, but many other chemical and physical agents can also cause gelation of colloids.

Membranes.—One of the most striking and significant properties of colloids is that they tend to form membranes at surfaces. Every cell is surrounded by a thin elastic sheet, the PLASMA MEMBRANE, which is composed of closely packed colloidal particles of proteins and lipins in the gel state. As we shall see, this membrane determines what shall pass into or out of the internal protoplasm. Numerous other membranes exist within the protoplasm at surfaces separating one kind of substance from another. Since membranes are rather firm and elastic, the more membranes present in a given mass of protoplasm, the more nearly solid will the unit be, and the more readily will it retain its shape. By way of analogy, it may be said that the solid consistency of mayonnaise dressing is due to the fact that a colloidal mixture of oil, water, and an acid (vinegar) is beaten up until a very fine mixture of the ingredient particles is obtained in which a membrane separates each particle of oil from the water. So many membranes are present that they

are almost continuous and the total mass is solid enough to hold its shape for some time.

Cell membranes are usually electrically charged either positively or negatively. A positively charged membrane repels positively charged particles or ions and prevents the latter from passing through its pores, but negatively charged particles or ions are attracted and may pass through the pores. Thus membranes through their chemical charges, as well as through their porosity, tend to control the passage of other particles through them. Many other substances pass through membranes by dissolving in the lipin components of the membrane. Alcohol, ether, and other anesthetics enter cells in this way.

Osmotic Pressure.—One of the most significant physical phenomena associated with colloidal membranes is OSMOSIS, a term that requires explanation. If we put a soluble blue substance like copper sulphate in water we see that the blue material, without any stirring, tends to diffuse slowly throughout the water until all molecules and ions are evenly distributed. If an impermeable membrane like a film of glass is placed between the blue solution and the clear water the diffusion is completely stopped, but if a membrane is used that is permeable to water but not to copper sulphate, the water will pass through and mix with the copper sulphate, but the latter cannot get through into the water. The addition of the water to the copper sulphate will increase the volume on that side of the membrane and will cause the membrane to bulge in the direction of the remaining water. The pressure thereby exerted is called OSMOTIC PRESSURE, which may be very powerful. Osmotic pressure plays a very important rôle in life processes. Many important phenomena in cells depend upon this semipermeability of their membranes. Red blood cells, for example, contain certain salts that cannot diffuse out but water can easily diffuse in. Normally, however, the concentration of electrolytes within the cell and in the blood plasma is equal. But if these same cells are placed in pure water, too much water enters through the membrane and they swell up and burst; while in solutions of salt more highly concentrated than those within the cell, water passes out through the cell membrane and the cell shrinks and becomes wrinkled. Cells are kept plump and well rounded because the osmotic pressure on the inside and on the outside of the plasma membrane is equal.

While other important physical properties of living matter and living units might be mentioned, it seems best to leave the subject at this level of difficulty.

E. Mechanism versus Vitalism

This seems the most appropriate place to introduce a brief discussion of one of the most vexed problems of biology. After getting a bit of information about the physical and chemical properties of matter, after being told that living matter is no more than an extremely complex form of matter, and that the activities of living things are the result of various kinds of transformations of energy, the student has a right to inquire whether or not all the phenomena of life are explainable on a purely physicochemical basis. Biologists are divided on this question into two schools: the MECHANISTS and the VITALISTS.

The Mechanistic Point of View.—A large majority of working biologists are mechanists. Experience has taught them that, as a working hypothesis, it pays to assume that vital phenomena are natural and result from the energy transformations going on in various peculiar kinds of material substances, protoplasms. Using the mechanistic working hypothesis, they have succeeded in gaining adequate understanding of a vast number of phenomena of life in terms of the physicochemical processes involved. They expect to hold fast to this working hypothesis so long as it gives fruitful results. At the present stage of rapid advance in our understanding of the mechanisms of life it would seem futile to acknowledge that there are vital phenomena that can never be understood in terms of physicochemical mechanisms. It may turn out in the end that such phenomena as thought, imagination, emotion will forever evade a mechanistic explanation, but this admission will not be forthcoming until progress in biological research based on the mechanistic hypothesis comes to a standstill. If, ultimately, this program of research fails, one will be justified in adopting the defeatist program of the vitalist, who admits at the outset that there is something unknowable about life.

The Vitalistic Point of View.—In the words of Woodruff: "The vitalistic conception holds that life phenomena are in part at least the resultant of manifestations of matter and energy which transcend and differ intrinsically in kind from those displayed in the inorganic world—a denial, as it were, in the organism of the

Animals	*Green Plants*
Capable of ingesting solid food.	All food taken in as gases or in solution.
Food substances their only source of energy.	Light their primary source of energy.
Excrete their waste products.	Use up their waste products, or "burn their own smoke."
Use most of their energy for active movement.	Use most of their energy in growth.
Hence decrease the amount of organic compounds.	Hence increase the amount of organic compounds.

From this list of differences the reader will readily gather that animals and green plants play a reciprocal rôle in maintaining the balance of energy in nature. Together they tend to maintain an equilibrium of the energy sources on the earth's surface, for they work into each other's hands, as it were. Most of us are familiar with a balanced aquarium containing fish and aquatic vegetation and know that such an aquarium tends to reach and to maintain a balance between the amount of animal and plant matter. Such an aquarium well illustrates the reciprocal relation between animals and plants.

B. Energy Cycles in Plants and Animals

Let us first take a close-up view of the energy traffic in green plants.

Photosynthesis.—As the term indicates, photosynthesis is the process of synthesizing compounds out of simple raw materials by the aid of light. In green plants the synthesizing agent is CHLOROPHYLL, the green substance so characteristic of plants. Chlorophyll has the power to absorb the kinetic energy of certain rays (chiefly those at the red end of the spectrum) of sunlight and to transform it into chemical energy—the potential energy of carbohydrates. The green plant takes in carbon dioxide (CO_2) from the air (or from the water in the case of aquatic plants) and water (H_2O) from the soil. Under the influence of light the chlorophyll acts as a sort of catalyst which combines water and carbon dioxide to form glucose. Free oxygen is a by-product of this reaction.

In chemical terminology the reaction is as follows:

$$\underset{\text{carbon dioxide}}{6\,CO_2} + \underset{\text{water}}{6\,H_2O} + \text{energy} = \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{free oxygen}}{6\,O_2}$$

Glucose, as we have seen, is one of the simplest of the carbohydrates and is the kind of fuel substance most readily used for energy production by protoplasm. The actual reaction is probably not quite so simple as we have indicated, but the result is as shown. In most plants glucose is transformed almost as soon as formed into the more complex carbohydrate, starch, which is stored in the form of starch grains, a reserve energy source for growth and respiration during the hours of darkness. Also some of the glucose is combined with ammonia (NH_3), derived from the dissolved nitrates of the soil, to synthesize a variety of amino-acids out of which the plant manufactures its own proteins. The only step in this series of events that requires light and chlorophyll is the first one, photosynthesis. The others can go on in the dark.

The primary significance of photosynthesis is that it is the main process in living organisms in which there is an actual increase of potential energy. The ultimate source of all new energy in organisms is sunlight. Animals, of course, depend ultimately on green plants for their food. Even purely carnivorous animals feed upon herbivorous animals, which in turn are dependent upon green plants. So in a very real sense sunlight is the ultimate source of vital energy.

Respiration.—In the present connection the word "respiration" does not mean the mechanical breathing of air but the chemical process of oxidation or combustion of substances in the protoplasm. Plant cells, like animal cells, so long as they are alive, continuously take in oxygen, combine it with carbohydrates (to some extent with proteins and lipins) and release as by-products carbon dioxide and water. The chemical reaction involved in the respiration of glucose is as follows:

$$\underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\substack{\text{free}\\\text{oxygen}}}{6\,O_2} = \underset{\substack{\text{carbon}\\\text{dioxide}}}{6\,CO_2} + \underset{\text{water}}{6\,H_2O} + \text{energy}$$

This, of course, is exactly the reverse of that given for the process of photosynthesis. Hence photosynthesis and respiration are reciprocal processes. Moreover, the same amount of energy from light which was bound up as potential energy in forming glucose is released when glucose is broken down by oxidation. This released energy is transformed partly into heat, partly into growth, partly into movement, and partly into reproduction, etc. No energy is left over or lost.

Now the nature of respiration in animal and plant cells is the same, the chief difference being that plants consume the water and carbon dioxide again, while animals excrete all of the latter and part of the former. Hence it is said that plants "consume their own smoke," while animals do not.

Respiration goes on as well at night as in the daytime, in contrast to photosynthesis. In a plant photosynthesis exceeds oxidation and therefore organic material is synthesized faster than it is used up. This is the explanation of continuous plant growth. Growth in animals is different in that it depends upon a more rapid building up of protoplasm from foodstuffs than the breaking down of the latter in respiration.

Metabolism.—This synthesizing, or energy expropriating process, together with the energy releasing and transforming process, constitute what we commonly call metabolism. We refer to the building-up phase of metabolism as ANABOLISM and the breaking-down phase as CATABOLISM. The two processes are so closely linked in all life activities that they are usually thought of as constituting a cycle of energy known as the METABOLIC CYCLE. But this is not the whole story of energy changes associated with living things. A more nearly complete story can be told by means of accounts of the two great energy cycles in nature, the carbon cycle and the nitrogen cycle.

The Carbon Cycle.—Since plants are continuously using up the somewhat limited supply of carbon dioxide in the air and since this is the only available form of carbon for photosynthesis, what is there to prevent the exhaustion of carbon dioxide? Of course some new carbon dioxide is produced during volcanic eruptions and in the combustion of coal and wood in fires, but this is utterly inadequate to keep up the needed supply. The main renewal of carbon dioxide is taken care of by organisms themselves, the most important of which are the lowly bacteria. Both animals and plants are continuously, as long as they live and grow, locking up carbon in organic compounds: carbohydrates, lipins, and proteins. Some of these are combusted and give off carbon dioxide, but much more of it goes into the structure of animal and plant bodies than is oxidized during their lives. After death, however, the bodies of plants and animals undergo decay, a slow type of decomposition carried out through the instrumentality of special kinds of bacteria, THE BACTERIA OF DECAY. Bacterial decomposition results in the

production of simpler organic products which in turn may be oxidized by atmospheric oxygen so as to produce carbon dioxide and other products, thus restoring carbon dioxide to the air. If it were not for these humble bacteria life would become extinct on earth, for before very long all the available carbon would be locked up in the dead bodies of animals and plants. In addition to respiration, all living things carry on another kind of decomposing process, FERMENTATION, which goes on more effectively in the absence of free oxygen. Thus the splitting of glycogen into lactic acid in the active muscle is a fermentation process, facilitated by a special

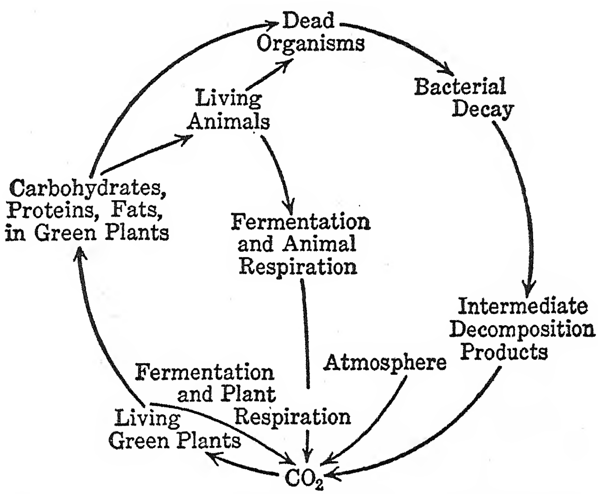


FIG. 25. Diagram of the Carbon Cycle. (From Woodruff.)

enzyme. Some of the lactic acid is then further oxidized. All of these modes of restoring carbon dioxide to the air balance the loss of carbon dioxide from the air through photosynthesis. Hence the total supply remains nearly constant, for the same carbon atoms that are used in the photosynthesis of glucose are ultimately returned to the atmosphere through a variety of processes carried on by living organisms themselves. The carbon cycle is diagrammatically illustrated in Figure 25.

The Nitrogen Cycle.—Even more elaborate than the carbon cycle is the nitrogen cycle. The reserve supply of nitrogen exists in the atmosphere in the form of an inert gas that ordinary living beings cannot use. The first step in combining nitrogen into a

usable compound is taken by certain nitrogen-fixing bacteria which combine nitrogen with oxygen and potassium to produce soluble nitrates. These organisms are of widespread occurrence in the soil or occur in the root nodules of leguminous plants, such as clover, alfalfa, peas, and beans. Crops of these plants are commonly plowed under to enrich the soil in nitrates. These soil nitrates are taken up by the roots of green plants and combined with carbohydrates to form plant proteins, which in turn are used by animals to produce their own proteins. As the result of the bacterial decay of both plant and animal proteins ammonia (NH_3)

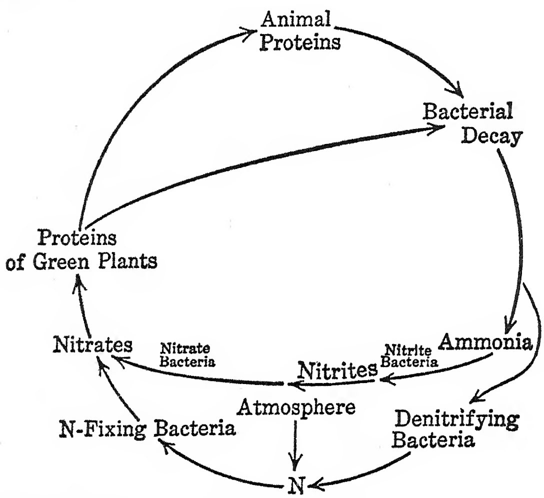


Fig. 26. Diagram of the Nitrogen Cycle. (From Woodruff.)

is released. This ammonia is taken up by three different sorts of bacteria. One sort of bacteria, called DENITRIFYING BACTERIA, break up the ammonia and release free nitrogen into the air, thus restoring it to its original source. The other sort of bacteria, NITRITE BACTERIA, combine the ammonia with oxygen to produce NITRITES. Still another set of bacteria, NITRATE BACTERIA, convert the nitrites into NITRATES, in which form they are taken up by green plants. One of these methods of disposing of ammonia short-cuts the cycle by omitting the free nitrogen stage, but the other method is used on a large scale and serves to keep the nitrogen supply in the air nearly constant. Figure 26 shows diagrammatically the various phases of the nitrogen cycle.

The dynamic equilibrium maintained by living organisms with respect to carbon and nitrogen illustrates the principle that the whole world of living things, animals, plants, and bacteria, are interdependent in very important ways. Each part of the cycle of work is essential for the well-being of the whole living world. From this point of view the whole world of life might be regarded as a huge organism, the largest of the life units possible on a single planet.

C. Modes of Obtaining Food Supply

(Parasites, Saprophytes, Symbionts, and Predators)

In the sense that they can manufacture their own food out of simple inorganic materials the chlorophyll-bearing plants are truly INDEPENDENT organisms. Some bacteria are believed to subsist on petroleum oil, but the latter is probably a product of the decay of organisms and therefore not truly inorganic. Also such bacteria as nitrifying bacteria, sulphur bacteria, and iron bacteria are able to get their energy directly from nonliving substances.

Most other organisms are DEPENDENT, in the sense that they must get their food directly or indirectly from the green plants. The various types of dependence are called parasitism, saprophytism, symbiosis, and predaceousness.

PARASITES may be defined as dependents that feed directly upon other living organisms. SAPROPHYTES live upon dead organisms or their decomposition products. SYMBIONTS live in or on other organisms in a mutually beneficial relation. PREDATORS capture living animals and eat them. It is comparatively easy to distinguish saprophytes from the other types. Thus fungi are usually saprophytic and so are many bacteria, such as those discussed in the carbon and nitrogen cycles. But other bacteria are considered parasitic because they inhabit living organisms. Even when they do invade the cells of living organisms, however, they do not feed directly on protoplasm: rather, they give off digestive enzymes which change protoplasmic materials into a form that may be absorbed by bacteria. Some parasites live in the digestive tract of the host animal and merely absorb part of its digested food. Still others thrive on the waste products of the host without doing any particular damage, some indeed being definitely beneficial.

When parasite and host live together to their mutual benefit, each furnishing the other with food or helping each other in other ways, the relation is known as SYMBIOSIS, and the participants in the arrangement as SYMBIONTS. It is often very difficult to make out a good case of mutuality for symbionts. The benefit to one party is usually clear, but that to the other somewhat doubtful. Frequently symbiosis borders on benign parasitism, that is, a condition in which the host tolerates the parasite and the latter does no damage, but also does no good. An interesting case of symbiosis is found between termites and certain wood-digesting protozoa. The termites feed largely on wood, which they themselves cannot digest, but their intestines are inhabited by certain protozoans that can digest wood. The protozoans probably use part of the digested wood themselves, but the main part is used by the termites. The protozoans are indispensable to the termites, but there is some question as to whether the former could live outside the intestines of the termites. At least they thrive well as digestors for termites and receive the benefit of room and board.

The distinction between the parasitic and the predatory relation is not very clear. When a small animal attaches itself to a larger animal and sucks its blood, sometimes even killing it, it is called a parasite. When a hagfish enters the mouth or gill openings of a fish caught in a net, and eats up the latter's insides, it is sometimes called a parasite, or at least a pseudoparasite, apparently because it goes inside to make its attack. Lampreys, relatives of the hagfish, attach themselves by a sucker-mouth to the outside of larger fishes and rasp off their flesh piecemeal, often killing their prey; yet even this mode of getting food is sometimes referred to as parasitic, or pseudoparasitic. Thus we see that the distinction between parasitism and predaceousness is rather finely drawn. It seems that a predaceous animal is considered to be a large creature that captures and kills other animals quickly and then feeds upon their flesh, while a parasite is a small animal that attacks a larger one without immediately killing it. This distinction is rather superficial at best. An animal that kills and eats plants is a HERBIVORE, one that kills and eats animals is a CARNIVORE. The latter is predaceous, the former is not. As elsewhere in biology, the attempt to classify organisms or processes into distinct categories fails, for we always find intermediate or indeterminate conditions.

In this chapter we have tried to cover only the major phases

of energy traffic in organisms. In a later chapter we shall consider in more detail the various types of animal food, their digestion and assimilation and their modes of transformation into various types of energy.

SUMMARY

1. The attempt to classify all organisms as definitely either plants or animals is futile. That large group of organisms with both plant and animal characteristics had best be termed primitive plant-animals.

2. A list of differences between animals and green plants is given, indicating that these two groups play reciprocal rôles in nature.

3. Photosynthesis, the most unique process in green plants, is particularly significant in that it is the most important, though not the only process involving an actual increase in potential energy. It is regarded as an up-hill process.

4. All animal life is ultimately dependent for energy upon the products of photosynthesis.

5. Respiration is a down-hill process in which potential energy is transformed into kinetic energy. It involves oxidation of materials with high potential energy and the production of by-products of low potential energy with a release of kinetic energy.

6. Metabolism consists of the up-hill phase (*anabolism*), which involves synthesis of simpler materials to form more complex materials, and the down-hill processes of *catabolism*, or the breakdown of complex materials into simpler ones.

7. In the carbon cycle plants, animals and bacteria engage in team work to maintain a constant supply of available carbon dioxide for life processes.

8. The nitrogen cycle involves still more elaborate teamwork between animals, plants, and bacteria, in maintaining the nitrogen equilibrium in nature.

9. Parasites, saprophytes, symbionts, and predators represent various modes of energy expropriation among organisms. It is difficult in some cases to draw sharp lines of distinction as to these modes of energy expropriation.

CHAPTER IX

THE CELL THEORY, ITS HISTORY AND ITS LIMITATIONS

A. THE CELL THEORY

Cells and Other Life Units.—In Chapter IV we discussed the various kinds of life units ranging from ecological complexes and societies down to filterable viruses and genes. We emphasized the idea that the INDIVIDUAL, whether composed of one or many cells, of one or many persons, of members of one or several species, is in a very important sense the most fundamental of the life units discussed. The cell, on the other hand, is generally recognized as the most uniquely characteristic of all vital units and has been raised to the rank of *the* life unit *par excellence*. Around this idea of the supreme importance of the cellular level of vital units has grown up a group of concepts which constitute what we call "The Cell Theory." The facts and theories about cells constitute a special branch of biological science known as CYTOLOGY.

In the historical chapter of this book the story of the discovery of the microscope and the resultant revelations as to cells has already been told. We have seen that the first clear and definite formulation of the Cell Theory was made by ***Schleiden*** and ***Schwann*** in 1839. Of the two, Theodore Schwann had by far the more penetrative intellect and saw much more clearly the far-reaching applications of the theory. In its extreme form the Cell Theory claims that all plants and animals are made up of cells; that all biological phenomena are, in last analysis, cellular phenomena. Thus variation, heredity, reproduction, are due to properties of cells. Furthermore, the individual is no more nor less than a society of cells, each in some degree dependent upon others. A protozoan organism is viewed as a single cell, equivalent to one of the cells of a metazoan organism, but merely more versatile in its activities and capacities. This extreme form of the Cell Theory has come in for much criticism, as we shall bring out later on in our discussion of the Organismal Theory. In spite of its limitations along these lines, the Cell Principle deserves to rank high among the Laws of Life.

B. The Cell Concept in the Making

The first conceptions of the essential features of a cell were crude and erroneous. *Hooke* and *Grew,* who first studied cells under the relatively low powers of their primitive microscopes, noted a sort of honeycomb texture in the tissues which they examined. Hence they applied the name "cell" to the unit of composition, doubtless influenced by the fact that the term had been used for the sections of honeycomb. Thus we see that the original concept of the cell emphasized the walls and practically ignored the important substances within them. More adequate technique revealed within the inclosure a nucleus, but this structure was thought to be part of the wall. The semifluid substances filling the cavity, which we now know as the essential living substances, protoplasms, were at that time thought to be only by-products of the cell. Even Schleiden, one of the founders of the Cell Theory, spoke of the cell contents as a kind of gum.

It is to ***Felix Dujardin*** (1801–1860) that we owe the first recognition of the importance of the cell contents. He studied this material, tested its solubility and chemical properties, and decided that it was a special cellular material which he named SARCODE. Dujardin did not, however, appreciate the full significance of his discovery, believing that this sarcode was found only among lower organisms. Further study, however, soon showed that this was a mistake. ***Hugo von Mohl,*** in 1846, during his studies of plant tissues, found a similar cell content and called it PROTOPLASM, a name used in a more limited sense at an earlier time by ***Purkinje. Von Mohl*** was responsible for bringing the term "protoplasm" into general use and hastened the development of the growing conception that protoplasm was common to all living tissues and was much more essential than the cell wall. It is to ***Max Schultze*** (1825–1874), more than to any other biologist, that we owe the establishment of the present conception of the essential protoplasmic organization of the cell. The organized mass of protoplasm *is* the cell. The walls and the various contained materials other than protoplasm are merely the manufactured products of cell activity.

Cell Products.—It soon came to be recognized that many tissues, such as bone and cartilage, are only partially cellular. In such tissues the cells are situated relatively far apart, separated by a

mass of nonliving material known as a MATRIX. This matrix, though not itself living, is produced by and excreted from the protoplasm and is therefore a cell product. Similarly, cellulose in plants, the hard shells of mollusks, arthropods, and many protozoa, are cell products.

The Cell Both a Structural and a Functional Unit.—The founders of the Cell Theory were purely morphologists and thought only in terms of structure. The concept of the cell as the morphological unit out of which all organisms are composed soon began to change. The rise and growth of the science of physiology and, within the last few decades, the rapid development of the science of genetics, have focused attention upon cell activities as over against mere matters of structure. Slowly there has come to the front the idea that the cell is the physiological unit, that the activities of an organism may be conceived of as the sum of the individual cell activities. Each cell is supposed to be a physiological unit performing a particular kind of work, and the resultant of these combined labors constitutes the life of the organism. We now realize that there is an interdependence among these cells, that cells can live and function normally only when in their proper relations to the other cells of the organism.

The Cell a Unit of Development and Heredity.—As the science of embryology progressed it soon came to be recognized as a general law that organisms, no matter how complex or massive they may be in the adult condition, have their origin in a single cell, the egg. This is not a matter of theory, for the entire developmental process may be watched step by step. The method of development is seen to be essentially that of the multiplication of cells by cell division, the forming of layers of cells, the production of folds and processes in cell layers as the result of regional inequalities in rates of growth, the migration of certain cells from one place to another, and the influence of one type of cell upon others. The whole infinitely complex process may be shown to be, in last analysis, a matter of cellular activity. The question as to whether the cells do it all or whether there is something at work more potent than mere combined cell activity, is a problem for future consideration.

The result of embryonic development is the production of a new individual more or less similar to the parent. The reason for this likeness is that each of them, parent and offspring alike, starts out from an egg, goes through parallel embryonic stages, and comes to

a stop at the same level of organization. The basis of specific resemblance is obviously to be found in the common start made by the two; for both parent and offspring come from germ cells that have the same or a similar protoplasmic organization, the same rate of cell division, and the same growth peculiarities. Even when we consider that an individual is the product of the union of two cells, an egg of the mother and a spermatozoön of the father, we see that its origin is cellular. Modern genetics has shown that the mechanism of heredity involves the assembling in the germ cell of hereditary materials of two strains and the assorting and redistribution of these cellular elements in very precise ways. Although we do not yet understand either the exact causes of or the driving forces operating this heredity machine, we realize that in last analysis it is a cellular mechanism.

For these and other reasons, the extreme advocates of the Cell Theory have come to be imbued with the conviction that it is the most important unifying concept of biology and that we must approach the solution of all our problems from the cellular standpoint.

C. The Far-Reaching Influence of the Cell Theory

The Cell Theory was the first of the great biological generalizations to be commonly adopted and it is to this great unifying principle that we owe, more than to any other, the first great advance of Zoölogy along truly scientific lines. This was the first idea broad enough in its scope to bring all of the facts of biology under its sway. All life came to be thought of as cellular. It is interesting to recall that the great master principle, Evolution, had only a very sparse following until after the publication of Darwin's *Origin of Species* in 1859, just twenty years after Schleiden and Schwann formally launched the Cell Theory. There is little doubt but that the gradual maturing of the Cell Principle paved the way for the acceptance at the hands of biologists of other fundamental generalizations; for the idea of the oneness of living organisms resulting from their cellular constitution suggested the idea that all cellular organisms probably had a common origin.

Cytology.—Out of the study of cells as units of organization there grew the study of the finer structure of the cell and its parts and the mechanisms of cell multiplication and heredity, a specialized branch of biology now in a mature state and known as Cytology. Today Cytology concerns itself particularly with germ cells,

but should not, and in reality does not, exclude from its scope the significant features of cells other than germinal.

General Physiology.—The study of cellular activities has developed along other lines into what we know as General Physiology, essentially cellular physiology as distinguished from the physiology of organs or systems. General physiology concerns itself with the structures and properties of cell membranes, their permeability to substances in solution, the phenomena of surface tension, the electrical state of the surface as compared with the interior, the transmission of stimuli from cell to cell or from one part of the cell to another. In other words, the subject of general, or cell, physiology has come to be almost synonymous with biophysics and biochemistry.

D. The Organismal Theory as Applied to Cells

The Cell Theory in its extreme form regards a multicellular organism as a community of cells each doing a particular job as a member of the community. According to this view the activities of the organism are no more than the sum of the activities of its component cells; the cells make the organism what it is and are responsible for all its behavior. This extreme form of the Cell Theory has been viewed with alarm by many modern biologists, who believe that there are properties of the whole that are more than the sum of those of the parts. You will recognize our old friend the Organismal Theory in a new rôle as a corrective for the extreme form of the Cell Theory. Probably few modern biologists hold this view of the extreme importance of cells against which the Organismal view was aimed, but there was much need of this corrective a few years ago.

The Cell Theory has long had its opponents. Even so eminent a scientist as *T. H. Huxley* once expressed the opinion that:

"They [the cells] are no more the producers of vital phenomena than the shells scattered along the sea-beach are the instruments by which the gravitative force of the moon acts upon the ocean. Like these, the cells mark only where the vital tides have been, and how they have acted."

Had Huxley known what is now known about cells he would not have degraded them to the status of dead shells on the seashore. Nevertheless he struck a note that has been echoed with various changes by many leading modern biologists. The opinions of two

leading American zoölogists will serve to illustrate what we mean by the organismal point of view.

In an important essay ***Professor E. B. Wilson*** says: "The only real unity is that of the entire organism, and as long as its cells remain in continuity they are to be regarded, not as morphological individuals, but as special centers of action into which the living body resolves itself, and by means of which the physiological division of labor is effected."

In a discussion of "Properties of the Whole" ***Professor F. R. Lillie*** states: "If any radical conclusion from the immense amount of investigation of elementary phenomena of development be justified this is: That the cells are subordinate to the organism, which produces them, and makes them large or small, of slow or rapid rate of division, causes them to divide, now in this direction, now in that, and in all respects so disposes them that the latent being comes to full expression. . . . The organism is primary, not secondary; it is an individual, not by virtue of countless lesser individuals [the cells]."

We may seem to have gone out of our way to attempt to place the Cell Theory in its proper perspective, but experience has led us to believe that just this type of corrective is needed.

SUMMARY

1. While it is recognized that there are many levels of life units, it is generally conceded that the cell is the most unique and fundamental type of life unit.

2. The earlier students of cells, under the leadership of Schleiden and Schwann, proposed the Cell Theory, according to which the cell was the only type of life unit. According to this extreme theory the whole organism and all of its activities were regarded as merely the products of individual cell activities. This theory has had a profound influence on biological thought and has probably been overemphasized.

3. The Organismal Theory represents a reaction against the extreme form of the Cell Theory. It holds that the organization of cells within the individual is responsible for many of the properties of the individual, that these are properties of the whole and not merely the sum of the properties of the separate parts, and that the organism uses the cells as materials for expressing its organization.

CHAPTER X

THE BEGINNINGS OF LIFE AND THE ORIGIN OF NEW LIFE UNITS TODAY

A. Historical Statement

We have discussed in some detail the various levels of life units, especially units at the cellular level. The visible structure of cells, the physical and chemical organization of cells, and the energy traffic in living organisms have also received our attention. We must have been impressed by the definiteness and specificity of structure and function in these marvelous units and, if we have inquiring minds, we must have asked ourselves many times how such units first came into being. Some of us may be satisfied with the traditional view that life units were the product of divine creation and that each kind of life unit was the result of a special creative act. Most independent thinkers, however, from very early times have been unwilling to accept so naïve an explanation as to the origin of living things and have attempted to account for the origin of life on natural rather than supernatural grounds.

Even the Greek natural philosophers such as Thales, Anaximander, and Empedocles had ceased to attribute the origin of life to supernatural causes and believed in the natural origin of living beings (see pp. 15 and 16). Their views, however, differed from those held at present in that they thought that new life was arising every day out of nonliving materials, while modern biologists believe that life at some time in the very distant past arose spontaneously (through natural causes), but for various reasons is not originating *de novo* today.

There are really two separate problems as to the origin of living things: *a*, the problem of the first beginnings of life on the earth, and *b*, the problem of the origin of new life units today.

B. The Problem of the First Beginnings of Life on the Earth

Since the idea of the importance of cells as fundamental life units has come to dominate biological thought it is not unnatural

that anyone trying to picture the first living thing would have before the mind's eye a minute cell emerging out of chaos, full fledged, as it were, and ready for life. It seems highly probable, however, that the origin of life presented no such startling event, but that there were many steps in the process, no one of which would constitute an abrupt transition from nonliving to living matter.

We now know that filterable viruses exist that are possibly much simpler than cells, but which possess the essential attributes of life. Some writers suggest that filterable viruses may be free genes or protogenes. Now it would be much easier to conceive of the original spontaneous appearance of viruses or free genes than of much more complex units such as cells. Estimates as to the relative sizes of virus particles, genes, and large protein molecules reveal them to be all of about the same general order of magnitude—all excessively minute. It has been claimed that both genes and virus particles can be no larger than would be an aggregate of a few (possibly half a dozen) protein molecules.

Now both genes and virus particles have the power to expropriate materials from their surroundings and to synthesize them into more of their own substance, and the particles grow, divide, and hence multiply themselves. In doing these jobs they are, to all intents and purposes, being alive. Both also pass on indefinitely their own specific characteristics. What more do we require of a thing in order to admit that it is a living being?

If we conceive of the origin of life in the form of minute particles, possibly at first no more than single molecules, it is not too difficult to imagine that combinations of these with one another, and unions with other sorts of compounds with which they could form harmonious combinations, could give rise at first to very simple cells comparable to the smallest of the bacteria or to bodies as little differentiated as the cells of blue-green algæ. As ***Allee*** has pointed out in his treatise on *Animal Aggregations,* it seems probable that even the smallest primeval living particles tended to form aggregations, for at all levels of life units aggregations have definite survival value as compared with isolated individuals.

The problem of the original appearance of life on the earth can never be attacked except through reasoning and speculation, for there is no way of obtaining direct evidence. Of course if we should ever be able to produce living organisms in the laboratory

out of inorganic materials, we could assume that life probably arose in nature's laboratory in a similar fashion. The artificial production of life, however, has not yet been accomplished, though some optimists predict that such a miracle is possible and will in the end be performed. In the absence of any direct evidence as to the manner of origin of life, various biologists have had to resort to pure speculation. The following are some of the leading theories about this problem.

Theories of Helmholtz and Kelvin.—These famous scientists have sidestepped the problem by suggesting that life on our own planet came from other planets where life was already present. They point out that some spores and seeds of organisms are capable of withstanding prolonged exposure to very low temperatures and some of them can keep alive at very high temperatures. Also it is known that the spark of life can smolder along even in the almost complete absence of moisture and oxygen. These facts are regarded by Kelvin as favoring the possibility that long journeys through space—say from one planet to another—might be taken by particles of living matter, and thus life might be passed from one celestial body to another. But even if we should accept such an explanation of the origin of life on our planet we would still be confronted by the problem as to how life first started somewhere. Moreover, of all the planets in our solar system the Earth is, at least at present, much the most favorable for the origin of life. So why not let life originate here?

Pflüger's Theory.—Starting in with the assumption that the earth was once in a superheated, incandescent condition, Pflüger conceives of the origin out of this hot mass of a combination of carbon and nitrogen atoms to form cyanogen (CN). This substance in process of formation takes up a very great deal of energy (has very high potential energy). Now this combination of elements forms the core of the protein molecule and accounts to a large extent for the peculiar properties of proteins. The adding of cyanogen (CN) to carbohydrates or other compounds lacking this substance is looked upon as the step where lifeless stuff became alive, for protein is regarded as the center of life of the living substance, protoplasm. Pflüger considers that the origin of cyanogen and its subsequent chemical union with carbohydrate-like substances were inevitable consequences of the great heat and subsequent slow cooling of the incandescent constituents of the primitive Earth.

Moore's Theory.—Moore also starts with a very hot Earth, gradually cooling off. The gradual cooling permitted a series of chemical combinations to occur between the elements. Those with the greatest chemical

affinity united first to form the most stable compounds. Thus oxides appeared as soon as the temperature dropped sufficiently to permit them to be stable; then carbonates were formed; then came various inorganic colloids, more complex and less stable. Finally, with the earth sufficiently cooled off to permit their origin and maintenance, the organic colloids appeared. These substances are characterized by their highly complex molecular structure, their relative instability, their slowness rather than explosiveness of reaction, and their ability to change their colloidal state under the influence of comparatively slight external stimulation. It is thought that many different kinds of organic colloids were formed but only some few were stable enough to survive as such. These formed aggregates of various sorts with one another and gave rise gradually to the first life units.

These and other theories have been seriously advanced by able scientists. However fantastic they may seem, they represent the best efforts of the human intellect to solve one of nature's most difficult problems. When all is said, however, we have to admit that the problem of the first origin of life is still completely unsolved.

C. The Origin of New Life Units Today

This second problem of the origin of life is far more nearly solved than the one we have just discussed, but there are still some aspects of it that are in doubt. The solution of this problem took a long time and has aroused an immense amount of controversy. The earlier biologists all believed in ABIOGENESIS (spontaneous generation), but nearly all modern biologists believe in BIOGENESIS (that all new life units today originate from preëxisting life units). We shall first deal with the theory of abiogenesis.

Spontaneous Generation (Abiogenesis)

The first natural philosophers believed that life arose spontaneously out of such nonliving materials as water and air, or from the interaction of earth, air, fire, and water. This process of generation was believed to be frequently repeated and to be a matter of everyday occurrence. Lowly creatures of all sorts were thought of as arising *de novo* out of previously nonliving materials, without any particular cause, i.e., spontaneously. Human beings were known to develop within the uterus of the mother, but the beginning of a new human being was supposed to be largely spontaneous or to depend upon an act of the gods. The

idea of ABIOGENESIS (SPONTANEOUS GENERATION) has been held persistently and is still believed by a few to hold good for the lowest organisms; but the vast majority of modern scientists have entirely abandoned this view.

The history of the origin and abandonment of the idea of the spontaneous origin of living organisms is of so great significance that we shall give it in some detail.

Among the Greeks we find that ***Thales*** believed that Mother Ocean was the parent of all life. ***Anaximines*** thought that air imparted life to all things. ***Aristotle,*** even though he knew that at least some animals arise from eggs produced by parents, asserted that "sometimes animals are formed in putrefying soil, sometimes in plants, and sometimes in the fluids of other animals."

In later times we find the poet ***Virgil*** describing in the *Georgics* what he evidently believed to be a practical method of obtaining bees by spontaneous generation:—

> "First, a space of ground of small dimensions is chosen; this they cover with the tiling of a narrow roof and with confining walls, and add four openings with a slanting light turned toward the four points of the compass. Then a bullock, just arching his horns upon his forehead of two years old, is sought out; whilst he struggles fiercely, they close up both his nostrils and his mouth; and when they have beaten him to death, his battered carcass is macerated within the hide which remains unbroken. Then they leave him in the pent-up chamber, and lay under his sides fragments of boughs, thyme, and fresh cassia. This is done when first the zephyrs stir the waves, before the meadows blush with new colors, before the twittering swallow suspends her nest upon the rafters. Meanwhile, the animal juices, warmed in the softened bones, ferment: and living things of wonderful aspect, first devoid of feet, and in a little while buzzing with wings, swarm together, and more and more take to the thin air, till they burst away like a shower poured down from summer clouds; or like an arrow from the impelling string, when the swift Parthians first begin to fight."

The reader will doubtless surmise that Virgil was less observant than poetic and described the emergence of bee-like carrion flies and not the spontaneous generation of bees.

Ovid extends the notion of spontaneous generation much farther in the following passage, which purports to expound the doctrine of the Pythagorean philosophers:—

> "By this sure experiment we know
> That living creatures from corruption grow:
> Hide in a hollow pit a slaughtered steer,

Bees from his putrid bowels will appear,
Who like their parents, haunt the fields and
Bring their honey harvest home, and hope another spring.
The warlike steed is multiplied we find,
To wasps and hornets of the warrior kind,
Cut from a crab his crooked claws and hide
The rest in earth, a scorpion thence will glide,
And shoot his sting; his tail in circles toss't
Refers the limbs his backward father lost;
And worms that stretch on leaves their filmy loom
Crawl from their bags and butterflies become.
The slime begets the frog's loquacious race;
Short of their feet at first, in little space
With arms and legs endued, long leaps they take,
Raised on their hinder parts and swim the lake,
And waves repel; for nature gives their kind,
To that intent, a length of legs behind."

That spontaneous generation was not merely an example of poetic license is emphasized by the fact that ***Van Helmont,*** a famous physicist and chemist of the sixteenth century, describes in a circumstantial way how mice could be spontaneously engendered by putting some dirty linen into a receptacle together with some grains of wheat or a piece of cheese. The same writer gives us the following amusing recipe for engendering scorpions—"Scoop out a hole in a brick. Put into it some sweet basil, crushed. Lay a second brick upon the first so that the hole may be perfectly covered. Expose the two bricks to the sun, and at the end of a few days the smell of the sweet basil, acting as a ferment, will change the earth into real scorpions."

Cardan, in 1524, declared that fishes were spontaneously engendered in water and that many animals are the product of fermentation. Other alleged authorities claimed to have seen with their own eyes the origins of certain animals out of various plant or inorganic materials. In rural communities everywhere today some persons believe that frogs originate in clouds and come down in rain and that mosquitoes arise spontaneously in stagnant water. Every one has doubtless been told that a black horsehair, if left for some time in a watering trough, will transform itself into a wriggling hairworm. Everybody believed, until ***Redi*** proved the contrary, that maggots were spontaneously generated in putrid meat. Redi in 1680 performed a classic experiment which showed the fallacy of this popular conception.

Redi's Experiments.—He had frequently observed the stages of decay in meat and had noted that, long before maggots appeared in it, flies hovered around and sometimes alighted upon it. Could the maggots be the progeny of the flies, he wondered. If the flies were prevented from reaching the meat by placing paper on the glass containers the meat putrefied as usual, but no maggots appeared. Instead of paper he then put a fine gauze over the meat which allowed the odors of decay to pass out. Flies, attracted by the odors of decay, buzzed and crawled about, laying eggs at some distance from the meat upon the gauze. The result was that many maggots hatched out upon the gauze but none upon the meat. This proved once for all that maggots are not spontaneously generated on meat. So conclusive was this experiment that it practically broke down belief in spontaneous generation in general.

Discovery of Bacteria.—The belief, however, took a new lease of life when, in 1683, ***Leeuwenhoek*** discovered bacteria. These lowliest forms of life were so small and simple in organization that it did not appear so unreasonable for them to be spontaneously generated as it was for frogs, fish, maggots, and other much larger forms. Gradually the belief gained headway that bacteria were the product of fermentation and decay of organic matter. Thus ***Needham*** in 1749 firmly believed that he was able to observe the spontaneous generation of bacteria upon a grain of barley kept in water in a carefully covered watch glass. We now know that the watch glass was not really so covered as to keep out the spores of bacteria that are ever present in the air. Many other experiments with increasingly fine technique were performed to test the possibility of the spontaneous generation of bacteria. Even within recent years ***Bastian*** (1905) in a large treatise on *The Nature and Origin of Living Matter* maintained that he had actually seen the

FIG. 27. Louis Pasteur.

origin *de novo* of bacteria in infusions which, he claimed, had been heated to a point that must have killed all life and which were afterwards kept sealed up so as to prevent the possible ingress of the spores of bacteria.

Louis Pasteur.—We owe it to Pasteur that the belief in spontaneous generation of bacteria was finally abandoned by scientific men. He devised for this experiment a type of flask, shown in Figure 28. The neck of the flask containing putrescible material was drawn out and bent into the shape of a V. This could be left open while the contents of the flask were thoroughly boiled, and even after it cooled, without any contamination from the outside air being permitted. All the air that entered the body of the flask had to pass through the tortuous passage and through the fluid of condensation contained at the bottom of the V. Under these conditions bacteria never appeared in the body of the flask.

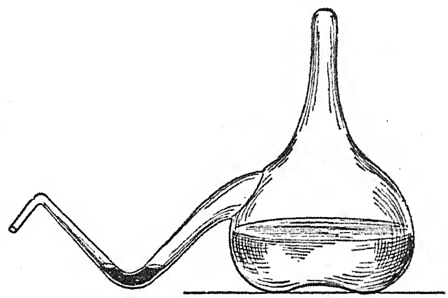


FIG. 28. Flask used by Pasteur in his experiments upon the spontaneous generation of life. Note that the top has been sealed after the contents have been poured in and that the bent neck is effectually protected from contamination by germs by means of the accumulated water of condensation. (From McFarland.)

Tyndall, with more elaborate apparatus (Fig. 29) and more detailed precautions against contamination, fully confirmed Pasteur's conclusions.

Bacteriological studies of ***Cohn*** and others have shown that bacteria under conditions of desiccation pass into a resting, or spore, stage and are capable of being carried about suspended in the air, ready to germinate under appropriate conditions. When, as in Bastian's experiments, bacteria appear in media that have been boiled for short periods and then bacteriologically sealed up, the only possible conclusion is that the spores have been heat-resistant to a degree higher than usual and have not been killed by the supposedly killing heat.

Conclusion.—It may now be stated with confidence that, with the world in the stage of development in which we find it today,

spontaneous generation of life is unknown and that the only way in which life is known to arise is through the reproductive capacity of living organisms already in existence. Harvey's dictum *omne vivum ex ovo* (all life from the egg), which had for a long time been accepted as valid for higher organisms, may be modified so as to include all organisms and be stated: *omne vivum ex vivo* (all life from preëxisting life). This may be called the principle of BIOGENESIS, one of the best established and most fundamental laws of life.

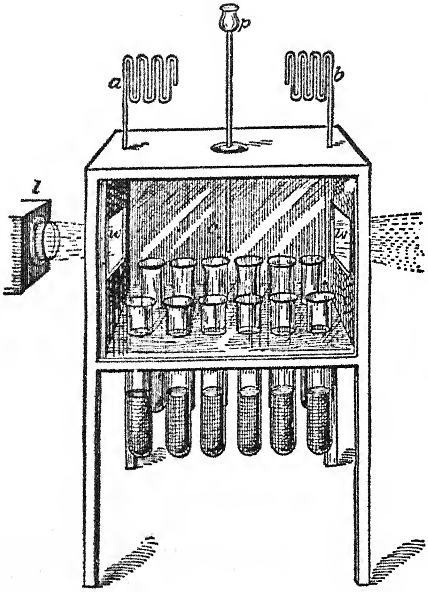


FIG. 29. Apparatus used by Tyndall for investigating the spontaneous generation of life. The front is of glass, as are the side windows, *w*, *w*. The optical test for the purity of the contained atmosphere is made by passing a powerful beam of light from the lamp, *l*, through the side windows. When the atmosphere of the chamber (*c*) contains no suspended particles, the tubes in the bottom are filled through the pipette, *p*. (From McFarland, after Tyndall.)

The question still confronts us, however, as to why, if life once started spontaneously, it does not sometimes start spontaneously today. One answer commonly given to this question is that the conditions (atmospheric, chemical, thermal, etc.) that prevailed at the time life arose are no longer possible, or at least do not now exist. One might suggest, however, that, with all our extensive laboratory facilities for producing any desired combination of environmental factors, we should be able to produce just the right conditions for inducing the synthesis of new life. Possibly some time this will be done.

Another answer to the question as to why new life does not arise spontaneously today is that offered by ***Chamberlin.*** He believed that life may well be taking the first steps toward spontaneous synthesis at various favorable spots, but the world is

already so full of all sorts of life forms, especially of bacteria, that a new, unfinished life substance would inevitably be the prey of these efficient feeders upon organic matter. In other words, the first steps toward the spontaneous origin of life, even if these occurred today, would inevitably be nipped in the bud by the ever present life units already existing. This view sounds reasonable, but at present there is no direct evidence in its support.

In conclusion, we may say that the weight of evidence favors the view that today all new life units arise from preëxisting life units. In the next chapter we shall show in detail how new cells arise from old cells. We shall see how the process of mitotic cell division affords an ideal mechanism for multiplying life units and at the same time preserving all the details of cellular organization so characteristic of any given species.

SUMMARY

1. The theories of natural and supernatural origins of life are contrasted.
2. The earliest life units to appear on the earth were probably much simpler than cells. Possibly life began at a level comparable with filterable virus particles or free genes.
3. The theories of Helmholtz and Kelvin involve the derivation of the first life germs from other planets, but this procedure merely transfers the problem to inaccessible regions.
4. Pflüger's and Moore's theories attempt to explain the origin of life units on a chemical basis. In both theories life units are regarded as arising as the inevitable consequence of gradual cooling of an originally fiery hot Earth.
5. Two theories of the origin of new life units today are contrasted: the theories of abiogenesis and biogenesis.
6. The history of the gradual abandonment of abiogenesis theories is given in some detail.
7. The theory of biogenesis, that today all new life units are produced as the result of reproduction of already existing life units, is now almost universally accepted.
8. The problem as to why new life does not seem to originate by abiogenesis today is discussed, though not solved.
9. The problem of the original beginnings of life is still unsolved.

CHAPTER XI

CELL DIVISION

A. The Problem of the Origin of Cells

For a considerable number of years after 1839, when the Cell Theory was formulated by Schleiden and Schwann, the problem as to how cells arise was still unsolved. The leading experts in cell study knew that some cells were produced by division of previous cells, but they also believed that cells sometimes arose by "free cell formation" as the result of a process resembling the origin of crystals in a solution. They believed that a cell might grow out of a nutritive substance by gathering to itself the necessary ingredients. Few examples of dividing cells had been observed, and it was believed that cells usually arose spontaneously in the manner described. This view of cell origin naturally prevailed so long as belief in the spontaneous generation of life held sway. If, they thought, organisms of some complexity could arise spontaneously out of nutritive media, cells should be able to arise even more readily in the nutritive media furnished by organisms. When, however, the ideas of spontaneous generation of life broke down under experimental demonstration, it at once became evident that cells, the units of life, must likewise arise from previously existing cells. Thus Harvey's dictum, *omne vivum ex ovo* (all life from the egg), was extended so as to fit the cell situation when ***Virchow*** in 1855 proposed the equally famous dictum, *omnia cellula e cellula* (all cells from cells), a dictum which is now considered a universal biological law.

B. Discovery of Cell Division and Progress in Our Knowledge of Its Mechanism

From the very first there was great curiosity about the mechanism of cell division, but little progress was made toward the discovery of its essential details for about a quarter of a century after Virchow stated the law of cell origin. Biologists were busy exploring the world of cells, bringing forth further evidence of the universal applicability of the Cell Theory. Microscopic tech-

nique, furthermore, had not reached the state of maturity necessary for the successful preparation of thin sections of tissues properly stained to show the details of cell division; nor had lenses of sufficiently high quality for visioning such fine details been devised. Progress in the study of cell division went along slowly because the investigators had to invent improved methods of preparing tissues for study and improved microscopes and modes of illumination.

A first crude attempt at a description of the events of cell division was made by ***Remak*** in 1855. His scheme was essentially as follows: The nucleolus first divides; then the nucleus follows suit, each part of the nucleus containing a new nucleolus; finally the cytoplasm divides into two equivalent parts, each with its nucleus, by means of a surface constriction which gradually cuts the cell into two cells. Though this process, which is equivalent to the mode of cell division known today as AMITOSIS, may, and probably does, occur in some tissues under some conditions, it is now known to be relatively rare. Further investigations under improved conditions soon showed that the usual method of cell division is far more complex than Remak supposed—in fact, one of the most complicated and difficult to interpret among elementary cellular phenomena. This complicated method of cell division came to be spoken of as INDIRECT CELL DIVISION as contrasted with Remak's scheme of direct cell division. Certain technical terms, however, have come to be applied to both methods. For the complicated or indirect method the names KARYOKINESIS (meaning nuclear activity) and MITOSIS (referring to the fact that at certain phases of the process the chromatin assumes the form of threads) have come into common use; while the direct method is called AMITOSIS (signifying the absence of any threadlike or fibrous condition of the chromatin). The terms mitosis and amitosis are now thoroughly intrenched.

In giving an account of mitosis one feels himself in the position of a showman who is able to present a series of pictures but can present no story that serves to explain the sequence of events or the underlying causes of the observed changes. If we could do so, we would take great pleasure in detailing for our readers the narrative of the events of mitosis with a running account of the physiological significance of each step and the exact value of each part in the division mechanism. It is unfortunate that at present

we cannot do this. The problem of the mechanism of mitosis is entirely unsolved. Later on we shall discuss some suggestions as to the nature of the mechanism, but we shall have to describe in a purely morphological fashion the more important scenes in the moving picture of mitosis. The process of mitosis is one of the most universal of biological processes, common to plants and animals, to the lowest and highest phyla of both kingdoms. No more fundamental vital process is likely to come to our attention. The process is one of those phenomena which may be thought of as expressing the essence of vital activity. If we could gain an adequate understanding in terms of physics and chemistry of mitosis, I suspect that we would not be far from a solution of the mystery of life.

C. The Events of Mitosis

While mitosis, wherever we find it, has certain universal features, considerable differences exist as to details, on the one hand, between that of animals and plants, and, on the other hand, among animals themselves. The account here given is that of the division of typical animal cells during cleavage, the period of cell multiplication in early embryonic development. This account will not apply to higher plants, for there we find no centrosome nor aster; neither will it apply without considerable reservation to cell divisions as seen in the Protozoa. The process of mitosis is a continuous one, really a cycle; for, starting out at any point in the series of events, we find ourselves coming back to the same point with the completion of each cell division. Even a continuous process, however, may be arbitrarily subdivided into periods, just as a drama may be subdivided into acts and scenes according to certain climaxes that serve as time markers of progress. Four periods in the process of mitosis have been distinguished and have been termed PHASES. These phases are: (1) the PROPHASES, including all of the events beginning with the first steps in division of the central body, the longitudinal splitting of the chromosomal threads, and culminating in the stage where the chromosomes lie in equilibrium in the equatorial plate; (2) the METAPHASE, the stage in which the chromosomes complete their longitudinal splitting and turn the half chromosomes to opposite poles of the spindle; (3) the ANAPHASES, the steps during which the half chromosomes travel toward the opposite poles of the spindle; and

(4) the TELOPHASES, during which the cytoplasm of the cell divides to form the two daughter cells, and the two chromosome groups are reorganized into the so-called resting nuclei, the equivalents

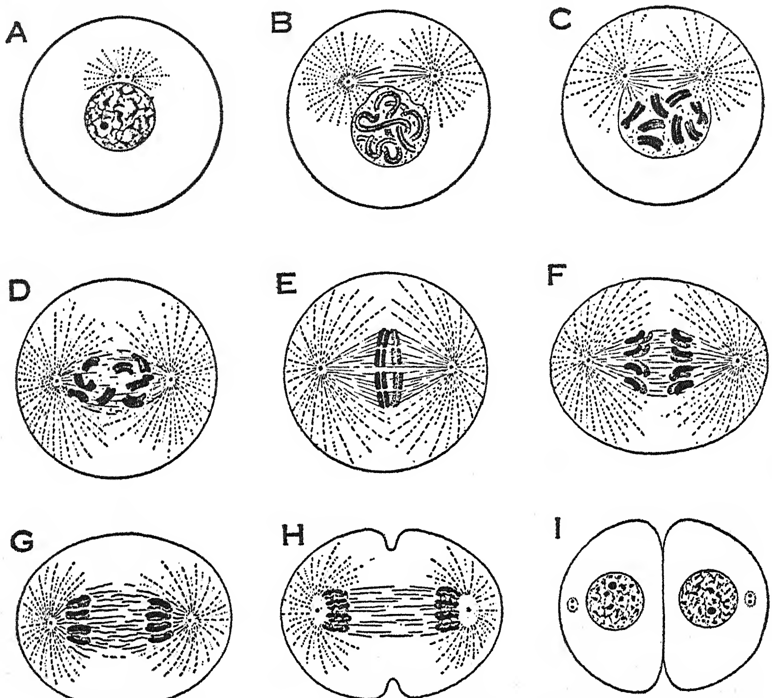


FIG. 30. Stages of mitosis as seen in embryonic cells, in which the chromosome number is eight. A, beginning of prophase, with chromatin in the form of a network and centriole divided and surrounded by aster; B, early prophase, with chromatin in spireme, long chromosomes already split lengthwise and centrosomes moving apart and forming a spindle between them; C and D, later prophases, showing disappearance of nuclear membrane and distinctly split chromosomes; E, metaphase, the twin chromosomes are lined up in the equatorial plate; F and G, early and late anaphases, in which daughter chromosomes are separating and going to opposite poles; H, beginning telophase, in which chromosomes are losing their clear outlines; I, mitosis completed, two daughter cells. (From Woodruff.)

of the original nucleus we started out with. And thus we have rounded out the cycle. A semidiagrammatic view of the phases of mitosis is shown in Figure 30.

We have now outlined what is essentially a drama in four acts, badly constructed from the artistic standpoint, for the climax, the

most important event of the whole plot, takes place in the second act at the metaphase, and the remaining acts are perhaps in the nature of an anticlimax. Relating the story of mitosis is like trying to keep track of several characters of a drama at once, for we have to note what goes on in the nucleus, especially the chromatin, what goes on in the central body, and what goes on in the cytoplasm. The story, on that account, will be a little disjointed, but the accompanying figures give "stills" at various stages so that we can see how each character has progressed. In the detailed account that follows, the illustrations represent the phases of mitosis of one species of clam, and are accurately drawn.

1. *The Prophases*

Between two periods of cell division the cell is in the so-called "resting stage." It is resting only in so far as division is concerned, for this is the period when metabolic activity is at its height and the cell grows from a half-sized to a full-sized unit. During this period the nucleus is spherical (Fig. 30, A) and the chromatin is arranged in the form of a fine network composed of scattered granules strung upon the threads of LININ. Some larger, deeply staining bodies lie within the nuclear membrane (Fig. 31). These are of two kinds, PLASMOSOMES and KARYOSOMES, the former being of unknown function, the latter being condensed masses of chromatin. At this time the centriole is seen as a pair of granules located in the middle of the central body. The first indication that a cell is about to divide is to be seen in the migration apart of the centrioles. As they do so they seem to spin between themselves a small spindle of fibers. Each central body also becomes crowned with a halo of radiating lines, which seem to have no solid consistency but are mere indications of lines of force emanating from the central body out into the cytoplasm (Fig. 31). While

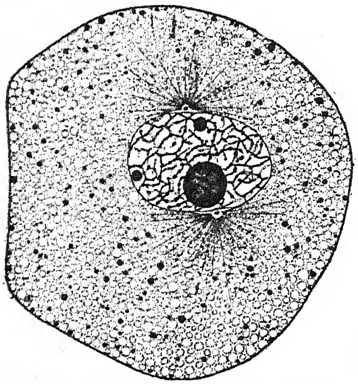


FIG. 31. Beginning of fourth cleavage division of egg of *Unio*. Centrosomes appearing on sides of nucleus. (From Dahlgren and Kepner.)

this has been going on, the chromatin in the nucleus has changed in appearance. It seems to have undergone a process of condensation, probably passing from a sol to a gel state, and appearing as a set of long thin threads coiled intricately into a close skein called a SPIREME (Fig. 32). These threads are usually already at least partially split lengthwise. Later the threads condense further, becoming shorter and thicker so as to form a series of long slender loops. By this time the two central bodies are far apart and the spindle clearly defined, with well-marked radiations from both central bodies. The whole mechanism of spindle and asters lies against the nuclear membrane and is known as the AMPHIASTER, or the ACHROMATIC FIGURE, because it is not composed at all of chromatin. Gradually the slender chromatin loops shorten and thicken to form a definite number of masses called CHROMOSOMES, which seem to be scattered at random through the nucleus. Up to this time the events inside of the nucleus and those associated with the amphiaster, outside the nucleus, seem to have been going on without reference to each other, but now the plot thickens. The nuclear membrane breaks down, possibly through the action of the forces resident in the central bodies; the spindle takes up its position where the nucleus had been, with the central bodies at opposite sides of the nucleus; and the chromosomes mingle among the spindle fibers, apparently attaching themselves thereto (Fig. 33). Slowly the chromosomes take up an orderly relation to the central bodies, migrating toward the equator and coming to lie in an equatorial plate equidistant from the two centrosomes. What impels them to take up this accurately balanced position we do not know, but will suggest

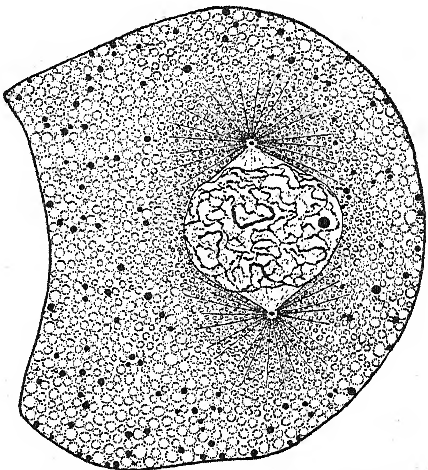


FIG. 32. Later stage than Fig. 31. Irregular spireme, centrosomes moving apart and nuclear membrane beginning to fail where touched by the forming spindle fibrils. (From Dahlgren and Kepner.)

certain possibilities later. The EQUATORIAL-PLATE stage marks the close of the prophases and ushers in the metaphase, the climax of the drama.

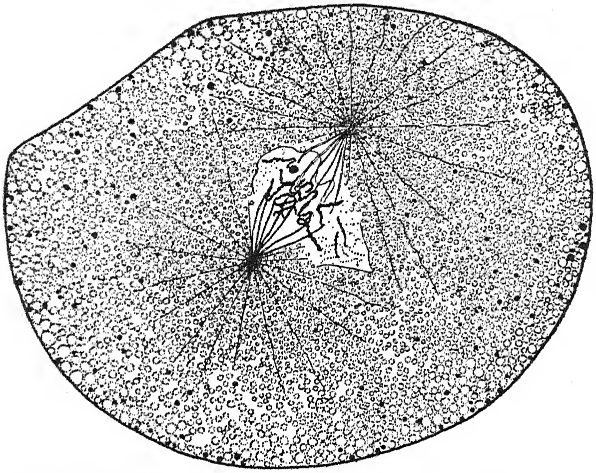


FIG. 33. Later stage of this mitosis. Nuclear membrane nearly gone. Spireme breaking to form chromosomes. Spindle fibrils growing toward each other. Nucleolus almost gone. (From Dahlgren and Kepner.)

2. *The Metaphase*

This phase is evidently one of equilibrium, for the chromosomes frequently rest there for a time as though balanced between two opposing forces (Fig. 34). During this period of equilibrium the chromosomes, if they have not already done so precociously, complete their division into two equal halves. The exact equivalence of the two pieces of each chromosome is a matter of considerable consequence, for it is upon the accuracy of this division that we base our conceptions of the mechanism of heredity. If chromosomes are highly individualized bodies, each carrying definite specific particles of substance that determine the characters of the individual, it is of prime importance that they should be divided in such a way as to maintain the integrity of their diversified composition and to insure its equal distribution to cell descendants. The mitotic mechanism appears to be ideally constructed to give these results. This fact lends added significance to the detailed study of mitosis. Some writers define the metaphase as no more than the period of splitting of chromosomes.

This definition breaks down in the case of many species in which the splitting takes place before the equatorial-plate stage. Moreover, the use of the word "splitting" for chromosome division carries false implications; as well use the word for cell division itself. The lengthwise division of chromosomes is a genuine reproductive process involving the growth and division of each of a long series of heredity units, genes, a series of which, like a chain

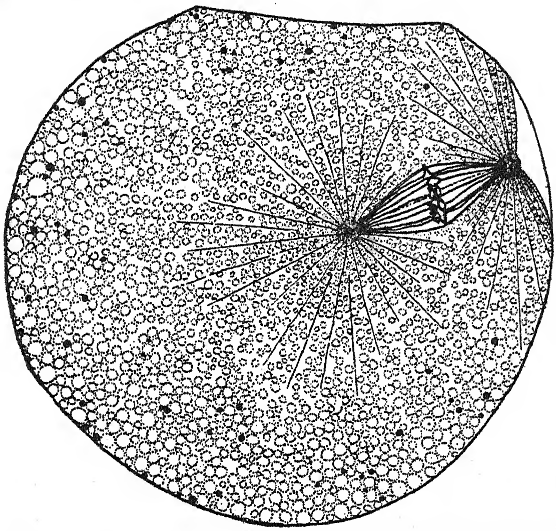


FIG. 34. Same process at time of formation of equatorial plate of chromosomes. (From Dahlgren and Kepner.)

of beads, occupies each chromosome. The arrangement of genes into chains is apparently a matter of quite secondary importance as compared with the highly specific character of the genes themselves. It is the twinning of genes, their division into equivalent halves, that constitutes the most important feature of chromosome behavior in mitosis.

3. *The Anaphases*

Soon after chromosome division is complete, the daughter chromosomes separate and drift apart from the equator of the spindle toward opposite poles (Fig. 35). Some go more rapidly than others; some lag behind after the rest have reached their destinations; but sooner or later they form two closely packed

groups about the two poles of the spindle. All of the steps in the process of distributing daughter chromosomes to their new locations, the centers of the prospective daughter cells, are anaphases. There is no exact point at which we can say definitely that the anaphases end and the telophases begin. The two processes are continuous. Usually it is during the late anaphases that the cell membrane begins to show the first signs of constricting to divide the cytoplasm. A slight furrow arises in the plane of the former equatorial plate and grows gradually deeper and deeper until it passes across the equator, which is marked by the presence of a plate of small granules indicating the site of the chromosomes when they were at the equatorial plate.

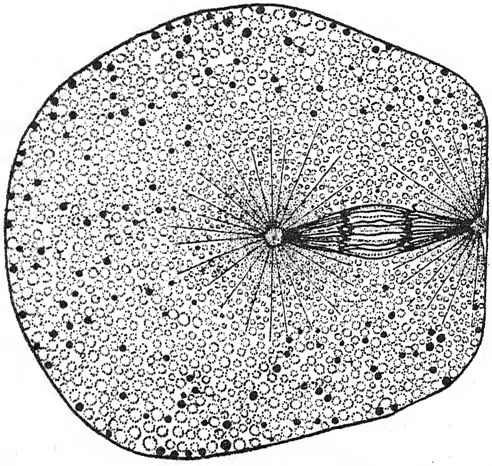


Fig. 35. A cell of the same kind showing separation of the chromosomes. (From Dahlgren and Kepner.)

4. *The Telophases*

This is the period of reconstitution of the normal vegetative condition of all the cell organs: nucleus, cytosome, central body (Fig. 36). The half cell becomes a whole cell with a complete membrane surrounding it; the nucleus becomes spherical and acquires a nuclear membrane; the chromosomes gradually reverse the order of their former changes, becoming less and less dense until they return to the condition of an apparent reticulum of granules strung on linin fibers. The achromatic figure is slow to disappear; even after the cells are completely cut apart, portions of the spindle fibers are to be seen in their original locations. The astral rays, however, disappear promptly and completely, leaving the central body of each cell in the original compact form in which we first saw it. Thus the little mitotic machine has retired into

small scope and remains inconspicuous until the approach of the next period of division.

The process of cell division, a simple reproductive event, may now be considered as completed. Now ensues the other phase of the cellular life cycle, that of growth. Growth has been in abeyance during the period of division, so that each daughter cell is but a half-sized cell. It now proceeds to feed and to grow till it reaches the maximum size limit of cells of its kind. Then it must divide again in order that growth may continue.

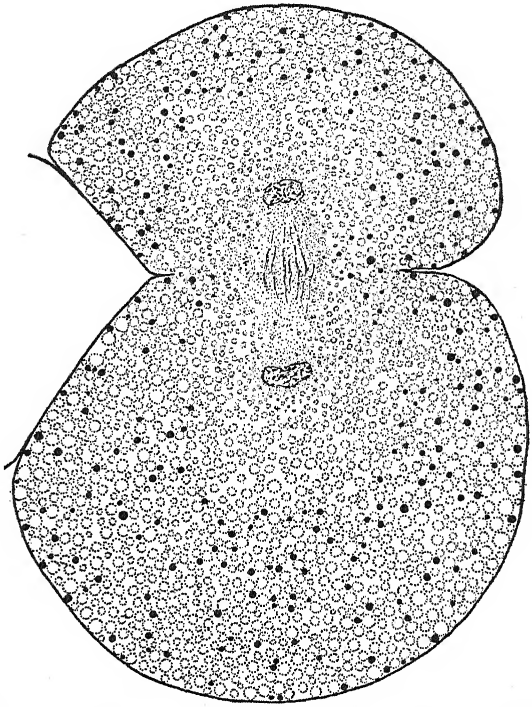


Fig. 36. Division of nucleus almost completed. Cell beginning to divide. (From Dahlgren and Kepner.)

The above account of mitosis is a generalized one based on the usual conditions seen in animals. There are, however, many exceptional forms of mitosis, a few of which will now be dealt with.

D. Various Types of Mitosis

The commonest departures from the typical condition described above have to do with the absence of central bodies. The higher plants present a naked spindle with neither centrioles nor asters. The maturation spindles of vertebrate eggs seem to be very much like those of the flowering plants. Thus the first maturation spindle of the mammalian ovum is clearly without asters and its central body seems to be no more than the point of convergence of

the spindle fibers. Another important variation from the norm is seen in species of Protozoa, e.g., Euglypha, in which the whole spindle forms inside of the nuclear membrane and the entire process of division is confined to the nucleus.

E. Numbers and Significance of Chromosomes

Mitosis seems to be primarily a mechanism for multiplying and accurately distributing chromosomes. There is ample evidence that the chromosomes are the bearers of hereditary materials called determiners or GENES. Hence the mitotic mechanism, including the chromosomes, may be thought of as the "heredity machine." There is now little doubt but that the chromosomes are qualitatively different and that each stands for a definite set of factors in heredity. It is of some interest to note that there is a constant number of chromosomes for each species, the number ranging from as low as two for the nematode worm, *Ascaris megalocephala univalens*, to sixty-four for the crustacean, *Artemia*, and even higher numbers in various animals and plants. The now famous fruit fly, *Drosophila melanogaster*, whose chromosomes are better known than those of any other animal, has 8 chromosomes; while man, according to leading authorities, has 48. In the section on *Genetics* we shall deal at greater length with the rôle of chromosomes in heredity.

F. The Problem of the Mechanics of Mitosis

It has already been intimated that our knowledge of the events of mitosis is at present almost entirely confined to a description of appearances. In other words, we know something about the morphology of mitosis, something about the importance of its rôle in development and heredity, but nothing very definite about the physiology of the process. What are the forces at work that make the central body divide and the two products migrate apart? What substances give rise to the spindle fibers? What causes the chromosomes to undergo progressive condensation and to migrate first toward the equator of the spindle, to divide lengthwise, then to leave the equatorial plate and migrate toward the poles? What causes the constriction of the cell membrane? These and many other questions of a physiological character remain as yet unanswered, but we are not without certain interesting and in some

cases valuable suggestions that may lead ultimately to a satisfactory solution of this extremely difficult problem.

Numerous observations have forced the conviction that mitosis is far from being a unitary process. The facts that nuclei often divide without any division of the cytosome, that spindles form without asters, that chromosomes divide prior to the formation of the spindle, indicate that the whole complex process of mitosis may be merely a coördination of a group of autonomous processes, each of which may be relatively simple in itself and capable of an equally simple explanation. If this be true, it would be futile to attempt to explain on physicochemical grounds the whole mitotic complex as a single mechanism. If we can explain the mechanism of one part at a time we may arrive at an adequate explanation of the whole.

Numerous theories have been devised to account for the nature of the asters and spindles, the reason for the constriction of the plasma membrane in the equatorial region, the nature of the spindle fibers and how they effect the migration of the chromosomes to opposite poles, why the cell elongates prior to cleavage. Some of these theories may with profit be briefly outlined.

a. Electromagnetic Theories of the Mitotic Figure.—There is a striking resemblance between the picture of mitosis in the metaphase and that presented when iron filings scattered evenly on a piece of paper are subjected to the forces emanating from the poles of an electromagnet. A spindle-like series of rays extends between the two magnetic poles and aster-like radiations extend out from the poles for some distance. According to one theory, we may view the changes in the cell and its ultimate division as the result of changes in the chemical constitution of various parts of the cell, resulting in electrical changes necessitating changes of shape and position of parts in order to restore equilibrium. The close resemblance of the mitotic figure to a field of polarized electrical forces may be merely illusory, but is at least very attractive.

b. Theories of Diffusion Streams and Surface Tension.—According to these views, of which there is a considerable variety, the astral rays represent lines of diffusion currents or lines of protoplasmic flow. Currents have actually been observed in favorable material, and it is known that the direction of flow is centripetal, that is, from the periphery toward the center of the

asters. This involves an accumulation of materials in the central bodies and the consequent growth of the latter as mitosis progresses. With the migration of more solid materials from the surface and from the equator of the cell toward the two central bodies, there is a resultant change in surface tension. This might account for the elongation of the cell in the axis of the spindle and for the constriction of the cytoplasm at its weakest point, between the two central bodies.

c. Theories of the Relation of Viscosity Changes to Mitosis.— These theories are intimately related to those just discussed and seem to supplement them. It has been pointed out by various observers that marked changes in viscosity of the protoplasm occur during the course of mitosis. There appear to be two periods of maximal viscosity, one during the prophases, the other just before the final step of cleavage. Relatively low viscosity prevails between these two points. Microdissection has revealed the fact that the astral rays are most viscous in the center and progressively less viscous toward the periphery. These and other observations have led to the conclusion that the aster is a sphere of solidification which extends its diameter as mitosis proceeds. The growth of two large solid regions tends to elongate the cell and to leave only one relatively fluid region, that between the two central bodies. Constriction occurs in this region because of changes of surface tension and in response to the tendency for the somewhat fluid outer portions of the cell to regain the spherical form.

At the present time there is no complete or adequate explanation of the mechanics of mitosis, but there is no reason for discouragement, for these problems are among the ultimate problems of life and we must be satisfied with progress in the direction of their complete solution, but must not expect such a solution very soon.

SUMMARY

1. All biologists now accept Virchow's dictum *omnia cellula e cellula,* implying that every living cell today has come into existence through a process of division of a previous cell.

2. The earlier observers of cell division described the process as a mass division of first nucleolus, then nucleus, and finally cytoplasm. Such a process seems to take place in later stages of some somatic cells and is called amitosis.

3. The type of cell division that seems to be normal, in the germ cell cycle at least, is called mitosis. Synonyms for mitosis are karyokinesis and indirect cell division.

4. The process of mitosis is usually divided into four phases: prophase, metaphase, anaphase, and telophase.

5. The most important event in mitosis is the splitting of each chromosome lengthwise into two exactly equal pieces, one of which goes to each daughter cell. This insures the heredity from cell to cell of the genetic complex characteristic of the zygote.

6. The spindle and asters are regarded as parts of a mechanism which helps to accomplish the meticulous passing on to each daughter cell of the hereditary materials of the zygote.

7. The number of chromosomes and their contained hereditary units, the genes, is constant for a given species, but varies greatly from species to species.

8. Very little is definitely known as to the exact mechanisms of mitosis. We can see the process in considerable detail, both in living and in fixed material, but we do not yet know what are the physical and chemical changes that lie beneath the pictures that we see.

CHAPTER XII

VARIETY, UNITY, AND ABUNDANCE OF LIVING ORGANISMS

A. Variety with Underlying Unity

One of the most characteristic properties of living things is their extraordinary variety. As a matter of fact, no two individuals belonging to the same species are exactly alike. Never are the offspring of the same parents very closely similar. Even so-called identical twins differ in many minor details.

A million or more different kinds or species of living organisms are recognized, and doubtless several times as many different species have lived in the past but are now extinct. The various kinds of organisms range in size all the way from the submicroscopic virus units (if such units actually exist) to the enormous whales.

This extreme diversity of animals and plants is so great that it would be utterly confusing were it not that beneath this diversity there lies a sort of unity and order. It is this unity and order that makes possible the systematic study of the animal kingdom.

Even the least experienced observer notes that some kinds of organisms possess certain features in common and differ in these features from other kinds. Every one has noted that deer, elk, moose, and antelopes have more in common than these animals have with cats and dogs. From such casual observations as this have arisen various systems of classification, the earlier ones based on superficial resemblances, the modern ones upon more deep-seated and fundamental resemblances. By classifying animals into groups we can think of the group characters as an abstraction and save our memories the labor of retaining separate pictures of all the different members of the group. It is this peculiarly human power of forming group concepts, that enables us to look over the world of nature and recognize all the forms we see as expressions of a relatively few general categories.

To get the proper feeling for biology every student should try to acquire the attitude of a naturalist. A naturalist is one who

sees nature broadly and is able to soften the focus of the mind's eye so as to catch an impressionistic glimpse of the whole. Let us then with the sweeping naturalist's eye glance over a couple of representative spots in nature's endless patchwork.

1. *The Tide Pools of Monterey*

One finds in the tide pools of the Pacific Coast, such as those near Monterey, California, examples of nature in some of her most lavish and kaleidoscopic aspects. If one has the opportunity to spend an hour or so in an examination of these pools, especially if the tide be more than commonly low, he will come away with the feeling that he has spent his time in a veritable animate museum. Almost all of the main groups of animals are represented in any pool of moderate size, and the numbers of individuals of many of the more conspicuous types exceed all expectation.

Perhaps the most obvious of all the peculiar forms are the echinoderms. The bottom is literally paved with purple and wine colored sea urchins, ranging in size from a quarter of an inch to six inches in diameter. The rocky walls and floors of the pools are decorated with the colorful forms of starfishes of several species, blood red, orange, yellow, cream, purple, gray, brown, and green. The twenty-rayed starfish, with soft, tentacle-like arms, adds a touch of weirdness to the scene.

Enormous numbers of mollusks, representing a great variety of orders and families, rival the echinoderms for supremacy as the dominant tide pool inhabitants. One can count in a few minutes scores of species of gastropods (sea snails). Conspicuous among these are the well-known abalone, the large Cryptochiton (the sea hare), and several kinds of nudibranchs; but more varied and numerous are the many species of limpets, chitons, and ordinary snails. Although not commonly an inhabitant of the smaller pools, the octopus is occasionally caught in them and thus isolated for a few hours from his usual haunts.

Almost equally in evidence are the crustaceans. Crabs of various sorts scramble over to rocks or swim about in the water. Barnacles, degenerate relatives of the crabs, form rugged incrustations upon the rocks, their knifelike shells a menace to waders. Shrimps, isopods, and amphipods dart from shelter to shelter.

Marine worms of many sorts lend variety to the scene. Some crawl about with the wriggling wormlike motion that character-

izes their kind; others swim with graceful undulations through the water; still others—and these are the most interesting and attractive in appearance and the least wormlike in aspect—are the fixed, or sessile, tube dwellers, whose pink and orange plumes (branchiæ) wave gracefully about on their stems like rows of delicate flowers. One can hardly believe that these are animals at all until at a touch of the finger, the flower-like plumes are suddenly withdrawn into the shelter of the tube, only to blossom forth again when all is quiet.

The cœlenterates, too, are well represented. Giant sea anemones spread their broad tentacled faces as traps for the unwary, while innumerable smaller sea anemones spread their multicolored tentacles like gardens of flowers. An occasional spectral jellyfish floats jerkily by, propelling himself with rhythmic contractions of his umbrella-like body. All sorts of colonial hydroids, aided by incrusting sponges and bryozoans (moss animals) help to soften the contours of the rocks and form a miniature forest shelter for the hosts of microscopic animals—chiefly larvæ and protozoans—that make of the sea water a veritable "sea-soup" upon which many of the somewhat larger forms subsist.

Almost overlooked at first because they are so perfectly camouflaged, but far from being the least important elements in the intricate complex, are the tide pool fishes that take toll of most of the edible small fry.

In addition to all of these strange and interesting creatures—and we have named only a few of the most conspicuous of the tide pool organisms—are the seaweeds: kelps, sea lettuce, Fucus. These play the indispensable rôle of furnishing food for the herbivorous animals and of keeping the waters supplied with fresh oxygen, to say nothing of the fact that they give shelter to many of the more timid and retiring animals that haunt their fronds and their holdfasts.

While such an intricate complex of conflicting and struggling organisms may seem to the uninitiated observer to be nothing but confusion, the ecologist sees in it a settled order, a balanced community, holding its equilibrium from age to age.

2. *The Inhabitants of Two Square Feet of Soil*

As a companion study to the marine picture outlined above, let us look for a few moments at a little plot of dry land. An investigator of the United States Department of Agriculture, interested

in the problem of the food of birds, set out to discover just what animals and plants inhabit two square feet of soil to a depth of a bird's ability to scratch. In this little patch of meadow soil he found 1254 animal objects and 3113 plant objects. These consisted of a great variety of kinds of living creatures. One kind of soil inhabitant that few persons have ever seen or even suspected the existence of is the group known as nematode worms, tiny little threadworms whose sheer numbers open our eyes to unexpected vistas of the limitless myriads of living things.

In a monograph on these animals, *N. A. Cobb,* a leading student of the group, says:—

"Not the least interesting thing about nematodes is the astounding variety of their habits. They occur in arid deserts, on the bottoms of lakes and rivers, in the waters of hot springs and in polar seas where the temperature is constantly below the freezing point of fresh water. They were thawed out alive from Antarctic ice in the far south by the Shackleton expedition. . . . A thimbleful of mud from the bottom of river or ocean may contain hundreds of specimens. The nematodes of a 10-acre field, if arrayed in single file, would form a procession long enough to reach around the world. A lump of soil no larger than the end of one's thumb may contain hundreds, even thousands, of nematodes, and yet present few points that would distinguish it from a lump of soil destitute of these organisms. . . . In short, if all other matter in the universe were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. The locations of the towns would be decipherable, since for every massing of human beings there would be corresponding massing of certain nematodes. Trees would stand in ghostly rows representing our streets and highways."

3. *The Prodigality of Life*

Innumerable as are the animals in every nook and cranny of the world, there seems to be no limit to the urge of life to multiply and to increase itself. Always more and more creatures of every sort are being born and there is a constant oversupply, a prodigality of wastefulness, which means a constant struggle for existence. Perhaps we may see with Darwin the value of overproduction in

that it gives nature a chance to select the best and throw out the poorest; thus may the standard be maintained or even improved. The world is now so running over with life that only those types or those individuals that can succeed in meeting the conditions of competition persist and leave offspring. Thus we can understand, with Darwin, why all living things seem to be so well adapted to the conditions of life; for how could a poorly adapted form have come through these ages of struggle till now?

We have now with the sweeping naturalist's eye looked, with vision not too sharply focused for details, over the world of teeming life. We have noted its amazing variety and almost inconceivable abundance. We see that the earth's surface is not only a lithosphere and an aquasphere, but a biosphere as well; for there is an almost unbroken layer of life covering the surface of the globe.

We cannot avoid a feeling of utter confusion in the face of such a complex world of life. Our way out of the confusion is through classification, as we shall soon see.

4. *How Classification Begins*

Let us examine another area of the biosphere, far separated from the one we have just pictured on the California coast. If we were to visit the rugged coast of Japan we would find there also tide pools much like those around Monterey. In these pools we would find the same teeming abundance and almost limitless variety of organisms, but we would be at once struck by the fact that they consist of much the same main kinds with which we have become familiar in the tide pools of Monterey. We would recognize many kinds of starfishes and sea urchins, all sorts of sea snails, numerous crabs and other crustaceans, many kinds of marine worms, sea anemones and their allies, colonial hydroids, and jellyfishes. If we were to use the microscope we would find again representatives of all sorts of minute forms resembling those in our own waters. Also we would find numerous fishes camouflaged to resemble their backgrounds. And finally, we would recognize a great variety of marine plants that remind us of American types. But while we would be struck by the fact that the two far-distant tide pools harbor much the same kinds and variety of organisms, living in much the same relations to each other, we would be even more forcibly struck by the fact that none of the many kinds of organisms in the Japanese pools are quite the same

as our own. All the Asiatic sea urchins, though obviously sea urchins, are different from the American ones in all sorts of details. The same is true for the snails, sea anemones, and all other kinds of animals. As soon as we use the expression "kinds of animals" we are introducing the group concept and have taken the first step in scientific classification. If we make the observation that two or more different kinds of sea urchins occur we are carrying classification a step further. Proceeding thus we subdivide groups into smaller and smaller subgroups until we arrive at a unit of classification that seems indivisible except into individuals. Such a group we call a *species*.

B. General Principles of Classification

Ever since the time of Aristotle, as we have seen, biologists have attempted to lump all animals into a few great groups separated from one another on grounds of various distinctive combinations of characters. It was long ago recognized that all animals were constructed according to a relatively few fundamentally different sets of specifications or body plans. Thus there is body plan I for Vertebrates, body plan II for the group called arthropods (insects, crayfish, spiders, etc.), body plan III for mollusks (snails, clams, squids, etc.), body plan IV for annelids (earthworms, clam-worms, etc.), body plan V for echinoderms (starfish, sea urchins, etc.), and about as many additional main body plans.

Each of these body plans has a different set of specifications. Thus the main specifications for body plan I, that for vertebrates, are about as follows: Bilateral symmetry, internal segmentation, internal skeleton consisting of a backbone and a brain case, a tubular central nervous system on the upper (dorsal) side, gill slits at least in embryos, etc. The specifications of plan II for arthropods are very different: bilaterally symmetrical, only an external skeleton, jointed appendages, external and internal segmentation, nontubular central nervous system on the under (ventral) side, etc. The specifications for plans III, IV, V, and the rest are about as different from one another as plan I is from plan II.

Now what is the biological significance of these so-called body plans? One view is that the Creator worked according to a few ideal plans and made all kinds of animals in essentially their present form through as many separate creative acts. The other view is that all those kinds of animals possessing a common body

plan have descended from a common ancestral type that used this plan, and that all its descendants have inherited the main specifications of this plan, each elaborating on it in its own peculiar way in accord with the various necessities of life. The first view is that of SPECIAL CREATION, the second that of ORGANIC EVOLUTION. Experience has shown that the first is unacceptable in the light of the evidence of nature and that the latter is well supported by such evidence, as we shall see later. We shall therefore accept evolution as our guiding principle in the study of classification.

All those life forms that are constructed according to one of these main body plans are grouped together into a large division known as a PHYLUM, the implication being that they have descended from a common ancestor, but have diverged along various special lines. Within the main Phylum we are able to detect groups of animals more like each other than like other groups. Thus among the members of body plan I, vertebrates, we find several large subgroups: cyclostomes, fishes, amphibians, reptiles, birds, and mammals. Each of these has distinctive characters (over and above those belonging to the main body plan) in which they differ from one another. We call these second grade divisions CLASSES. Each Class, in turn, consists of smaller groups, like one another in certain respects and differing from other members of the Class in these respects. That Class of vertebrates called mammals, for example, is subdivided into carnivores, ungulates (hoofed mammals), bats, whales, primates (including monkeys, apes, and man), and several others. These subdivisions of a Class are called ORDERS. Similarly, each Order is divided into several FAMILIES and each Family into several GENERA (singular, GENUS). Finally, a Genus consists of a number of SPECIES, the Species being the lowest standard unit of classification, although a Species may often be divided into SUBSPECIES and VARIETIES.

Now when we attempt to classify all animals into such categories as Phyla, Classes, Orders, Families, Genera, and Species, we always find some types that are difficult to pigeon-hole, for they may possess characters partly like one group and partly like another. Sometimes they possess a few of the main specifications of a major group, but lack others. When such forms are found they are considered as belonging to the group that they most closely resemble and are regarded as somewhat distant relatives of the

more standard members of the group in question. For example, we have discovered a number of curious animals that have a few of the distinctive specifications of vertebrates but are lacking in others (such as backbone and skull), but they have a notochord (predecessor of the backbone), gill clefts, and dorsal central nervous system. These near-vertebrates are combined with the true vertebrates to form a Phylum CHORDATA and they constitute two, or possibly three SUBPHYLA, coördinate with the SUBPHYLUM VERTEBRATA. This proceeding may seem a bit arbitrary, as indeed it is, but the groupings attained are at least highly convenient for our purposes. One must never forget, however, that classification is man-made and not a product of nature. Our efforts at classification should, nevertheless, have the aim of revealing the plan of nature. We have reason to believe that human classification and natural classification coincide in their broad outlines, but there is still doubt about many details.

The Binomial System of Nomenclature

One of the important permanent contributions to science made by ***Linnæus*** (1707–1778) was his very useful scheme of naming species of animals and plants. Instead of using the common vernacular names for kinds of animals or plants, names that might vary with different languages and with different localities, he used Latin names, for Latin was and is a sort of universal language. Each of the different kinds of organisms that were recognized as distinct were described briefly and their diagnostic features noted. All animals that agreed with such a diagnosis and differed only in minor individual points are grouped together in a single SPECIES. A group of Species that agree with one another except in a few constant minor features were grouped into a larger subdivision called a GENUS. Linnæus always gave a double name to a kind of animal, a name including the Genus and the Species to which it belongs. The generic name comes first and the species name second. Thus modern man is called *Homo sapiens* and the domestic dog is *Canis familiaris*. The nearest relative of the dog, is the wolf, *Canis lupus*.

Linnæus recognized certain groupings above the genus level, but the upper levels of his classification were very unsatisfactory, hardly as scientific as those of Aristotle. A great deal of advance in scientific classification has been made since Linnæus and we now

have an adequate method for placing most kinds of animals in their taxonomic setting.

As an example of the somewhat elaborate formulation of the taxonomic status of a single species, let us look at the credentials of the common red squirrel:—

SUBKINGDOM—*Metazoa* (multicellular organisms)
PHYLUM—*Chordata* (the chordates)
SUBPHYLUM—*Craniata* (the vertebrates)
CLASS—*Mammalia* (the mammals)
SUBCLASS—*Eutheria* (viviparous mammals)
DIVISION—*Monodelphia* (placental mammals)
SECTION—*Unguiculata* (clawed mammals)
ORDER—*Rodentia* (the rodents)
SUBORDER—*Sciuromorpha* (squirrel-like rodents)
FAMILY—*Sciuridæ* (flying squirrels, marmots, squirrels, chipmunks, etc.)
SUBFAMILY—*Sciurinæ* (marmots, squirrels, chipmunks)
GENUS—*Sciurus* (tree squirrels)
SUBGENUS—*Tamiasciurus* (red squirrels)
SPECIES—*hudsonicus* (Hudsonian red squirrel)
SUBSPECIES—*loquax* (Southern Hudsonian red squirrel)

The majority of animals would have as elaborate a classification as this, and some have an even more imposing taxonomic setting. We need not fear, however, that it will be necessary to characterize all of our animal friends in this fashion. We do not care to place so difficult a hurdle before the uninitiated, for many of the veterans would come a cropper if required to give from memory a classification like that just presented.

C. THE MAJOR GROUPS OF THE ANIMAL KINGDOM

The two broadest subdivisions of the Animal Kingdom are *a*, PROTOZOA and *b*, METAZOA. These groups are so different in body plan that most biologists recognize them as belonging to two separate Subkingdoms. The body scheme of the Protozoa is that, though they are often quite complex and specialized, they are UNICELLU-

LAR, i.e., the individual consists of but one cell. The body scheme of the Metazoa, no matter how simple, is that they are multicellular, i.e., they are composed of many cells specialized for many functions. In the Protozoa the various specialized parts of the protoplasm perform different functions, the protoplasmic specializations being known as ORGANELLES, in contradistinction to ORGANS of Metazoa, which are composed of many specialized cells.

The Subkingdom Protozoa is divided into four main divisions which are commonly called Classes, though it would be consistent with the recognition of the subkingdom value of the group to call them Phyla.

The Subkingdom Metazoa consists of some dozen or more Phyla, some authorities recognizing more and some less. These will be listed and characterized in the next chapter.

D. The Basic Criteria of Classification

These large groups, Phyla, are separated from one another because of differences in certain sets of fundamental features of organization. Some of the more important of these differentiating criteria may be mentioned:—

a. Diploblastic versus Triploblastic Organization.—In one Phylum, Cœlenterata, the body is composed of two and only two primary layers of cells, ECTODERM and ENDODERM. An individual of this group consists of an outer layer or tube, the ectoderm which acts as a body wall, and an inner layer or tube, the endoderm, which is the digestive tract. The two tubes are united at the mouth, there being no other opening into the gut. The space between the two tubes is filled with jelly in which loose collections of cells may be found. In flatworms, too, the space between body wall and gut contains loose masses of cells that are not strictly in layers. In all the higher Phyla, in addition to ectoderm and endoderm, there is a third or intermediate layer of cells, the MESODERM, though the Platyhelminthes have this layer in a loose condition that is regarded by some biologists as not true mesoderm, but as MESOGLŒA. Cœlenterates are thus two-layered or DIPLOBLASTIC, and the other true metazoan Phyla (except possibly flatworms) are three-layered or TRIPLOBLASTIC. Flatworms are really intermediate between the two conditions.

b. Symmetry.—A very useful criterion for classification purposes is symmetry of some kind, or its absence. Many kinds of

organisms, especially Protozoa, are asymmetrical (without symmetry). Among symmetrical organisms we recognize four types of symmetry: *a*, UNIVERSAL SYMMETRY, where the organism is spherical and all radii from the center to the surface are alike (example, Sun animalcules); *b*, RADIAL SYMMETRY, in which the various organs and systems radiate out from the center like the spokes from the hub of a wheel (examples: jellyfishes, hydra, and in a sense, echinoderms); *c*, BIRADIAL SYMMETRY, in which the radii of a radially symmetrical form tend to lie in two equal groups, suggesting bilateral symmetry (example, comb jellies); and *d*, BILATERAL SYMMETRY, in which the parts of the body are paired and arranged on two sides of a SAGITTAL PLANE so that they are approximately mirror images of each other (examples: man, insects, worms, etc.). In radially symmetrical animals one can divide the body into equal halves by cutting through the center along any plane, but in bilaterally symmetrical forms there is only one plane (the sagittal plane) through which a cut could be made so as to divide the body into nearly equal right and left halves. All forms that have recognizable right and left sides are thus bilateral. It should be said, however, that perfect bilateral symmetry does not exist, the left and right sides being consistently different in various ways.

c. Metamerism.—A considerable number of Phyla have an organization that involves a segmental structure, or one in which many parts are repeated down the long axis. There are at least two main types of metamerism, probably developed independently of each other, the one found in annelids and arthropods and the other found in chordates and to some extent in echinoderms. In the latter the pseudoradial symmetry appears to have been derived from a simple type of metamerism. In metameric forms each segment in a series of repeated segments is called a *metamere*. When all or nearly all of the metameres are alike, the type is called *homonomous;* but when most metameres are specialized for different functions, the type is *heteronomous.*

d. Cœlom.—This structure is typically an open cavity lined with mesoderm and lying between the gut and the body wall. The presence or absence of a cœlom has long been considered as of prime importance in classification, dividing the whole of Metazoa into CŒLOMATA and ACŒLOMATA. Two distinct and different kinds of cœloms have arisen in the evolution of different Phyla: *a*, a type in which the cavity of the cœlom was once continuous with the

cavity of the primitive gut (ARCHENTERON) and hence the cœlomic cavity is derived from pouches pinched off from the archenteron; *b*, a type in which the mesoderm exists at first in the form of two solid cords derived by multiplication of two pole cells, and in which the cœlomic cavities are formed by secondary hollowing out of these solid masses of mesoderm. The possession of one or the other kind of cœlom furnishes the basis for dividing all of the higher Phyla into two separate assemblages, or two main branches of the ancestral tree.

e. Skeleton.—Another good diagnostic feature is found in the various different types of supporting structures found in different kinds of animals. In some Phyla there is no skeleton. Among those with a skeleton we distinguish groups with external skeletons (example, Arthropoda), those with internal skeleton (examples, some lower chordates, all vertebrates, and the larvæ of sea urchins), and those with both internal and external skeletons (examples, many vertebrates). The NOTOCHORD is a stiff, elastic skeletal rod that is found in the adults of some chordates and in the embryos of all vertebrates.

Shells are skeletal in function, but in some groups such as molluscs the shell is merely excreted by the surface of the body and is not really a part of the body.

f. Appendages.—Many groups of animals are provided with externally projecting parts that serve as locomotor organs, feelers, food seizers and manipulators, or sex organs. Vertebrates usually have just TWO PAIRS OF APPENDAGES, which are PAIRED FINS in lower aquatic forms, and LEGS, ARMS, WINGS, in terrestrial forms. The great Phylum Arthropoda is characterized by having JOINTED APPENDAGES with external skeleton, while annelids have non-jointed appendages, PARAPODIA.

g. Circulatory Systems.—A circulatory system is one that distributes nutritive materials to parts of the body far from the source of supply and carries blood or its equivalent. In two large Phyla of Metazoa the digestive system and the circulatory system are in one, and this double system is called the GASTROVASCULAR CAVITY (examples, cœlenterates and flatworms). In all higher forms there is a separation into two independent systems, one attending to digestion and the other to blood circulation. Thus the presence or absence of a separate vascular system is diagnostic of various Phyla. Then again the blood system may be CLOSED

(i.e., contained within definite vessels throughout its course) or OPEN (i.e., not so contained, but permitting the blood to flow out into blood sinuses). This open or closed blood system criterion separates several Phyla from each other.

There are many other characters of diagnostic value that could be listed, but those given are the most useful ones. It is not expected that the beginning student will at the present time appreciate fully the significance of all these criteria of classification. It should be of value, however, to have been introduced to some of the major features of animal organization before dealing with the various types of animals that illustrate these features. This brief list of the chief diagnostic criteria used in the classification of animals is given a practical demonstration in the next chapter, where first will be presented a synoptic classification of the animal kingdom with diagnostic description of the major groups and then a theoretical discussion of the broad lines of interrelationship that are thought to exist among the various Phyla.

CHAPTER XIII

SYNOPTIC CLASSIFICATION OF ANIMALS

A. Introduction

This chapter is intended to supplement the last chapter in attempting to get a bird's-eye-view of the animal kingdom before introducing the more detailed study of selected types of representative animals. It is not expected that the student will attempt to memorize the material here presented, at least not at this time. After completing the study of types the more ambitious students may wish to return to this chapter in order to master its more important parts. For the present, however, it will be valuable to every student to learn at least the names, external appearance, and main distinctive features of the Subkingdoms and Phyla, leaving the Classes for a later time.

In this classification we shall, arbitrarily perhaps, divide the whole animal kingdom into two Subkingdoms, Protozoa and Metazoa. If we give Subkingdom value to Protozoa we should, to be consistent, elevate the present Classes of Protozoa to Phylum level, and we shall so do. The Metazoa are divided into two main Divisions, Parazoa (without digestive tract) and Enterozoa (with digestive tract). We have left out of this classification the primitive plant-animals, those that seem to be intermediate between the Animal and Plant Kingdoms.

In the following classification an attempt has been made to simplify the description of the various groups by mentioning only the diagnostic characters. We shall present only the major groups, Subkingdoms, Divisions, Phyla, and Classes. In order to make this long, dry classification a little more vivid, small thumb-nail sketches of one representative of each Class (each Phylum for Protozoa and each Subphylum for three lower chordate Subphyla) will be introduced. The one type chosen will in each case be the most representative we are able to select.

In most of the illustrations of representative animals used in this chapter no attempt has been made to show any more than external appearances except in transparent forms.

B. Classification

I. SUBKINGDOM PROTOZOA

Unicellular animals, some solitary, others forming temporary aggregates, still others forming permanent colonies that approach the condition of multicellular individuals.

Phylum 1, Rhizopoda (Sarcodina).—Protozoa with pseudopodia, used in locomotion and feeding (Fig. 37).

Phylum 2, Mastigophora (Flagellata).—Protozoa with one or a few long vibratile processes used in locomotion or feeding (Fig. 38).

Phylum 3, Infusoria (Ciliata).—Protozoa with numerous, relatively short vibratile processes, cilia, used in locomotion and feeding (Fig. 39).

Phylum 4, Sporozoa.—Parasitic Protozoa without locomotor organs in adult; no mouth; food absorbed directly from host; reproduce mainly by spores (Fig. 40).

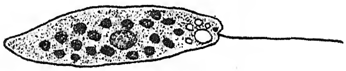


Fig. 38.

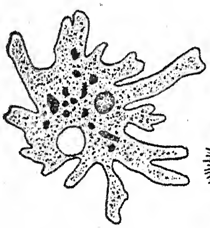


Fig. 37.

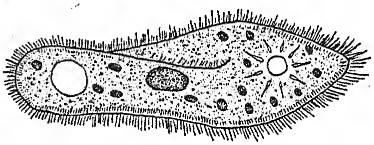


Fig. 39.

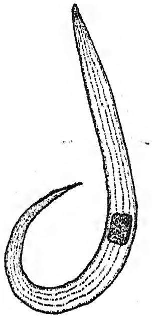


Fig. 40.

II. SUBKINGDOM METAZOA

Multicellular organisms in which the many cells are integrated to form units of a higher order.

DIVISION A. PARAZOA

Phylum Porifera (Sponges).—Metazoa without digestive tract (enteron); digestion intracellular; water and food particles carried into various passages through numerous pores, which play the rôle of mouths; whole organization utterly different from that of Enterozoa.

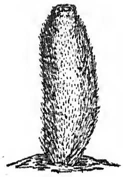


FIG. 41.

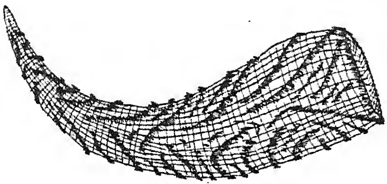


FIG. 42.

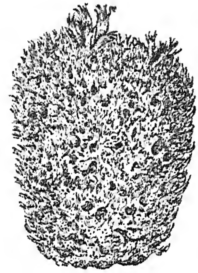


FIG. 43.

Class 1, Calcarea.—Sponges with calcareous skeleton composed of spicules; example, Grantia (Fig. 41).

Class 2, Hexactinellida.—Sponges with skeleton composed of six-rayed silicious (glassy) spicules; example, glass sponges (Fig. 42).

Class 3, Demospongia.—Sponges with skeleton composed of silicious spicules (not six-rayed) or of spongin, or both; example, common bath sponges (Fig. 43).

DIVISION B, ENTEROZOA

Metazoa with digestive cavity (enteron); having definite blastula and gastrula stages in their development.

PHYLUM 1, CŒLENTERATA.—Diploblastic, radially symmetrical, with gastrovascular cavity, mouth but no anus, always possess nematocysts (nettle cells).

Class 1, Hydrozoa.—Exhibit (typically) metagenesis, an alternation of generations between hydroid and medusa forms; frequently colonial with some colonies almost forming individuals of a higher order (Fig. 44).

Class 2, Scyphozoa (the larger jellyfishes).—In metagenesis the hydroid stage is inconspicuous and the medusa stage predominates (Fig. 45).

Class 3, Anthozoa (the corals, sea anemones, and sea-pens).—No medusa stage, the hydroid stage reproducing directly more hydroids; colony formation in some very conspicuous (Fig. 46).

PHYLUM 2, CTENOPHORA (sea walnuts or comb jellies).—Somewhat similar to Cœlenterata, but are usually triploblastic, are biradially symmetrical, and usually have no nematocysts (Fig. 47).

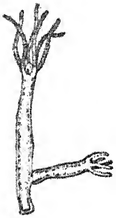


FIG. 44.

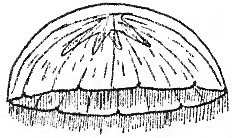


FIG. 45.

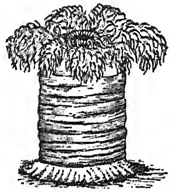


FIG. 46.

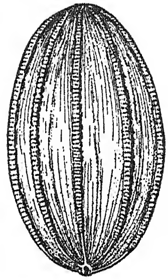


FIG. 47.

PHYLUM 3, PLATYHELMINTHES (flatworms).—Triploblastic, the third germ layer being a diffuse parenchyma; bilaterally symmetrical; no cœlom; a gastrovascular cavity; mouth but no anus; double ventral nerve cords.

Class 1, Turbellaria (free-living flatworms).—Leaf-shaped bodies; external surface covered with cilia; secrete mucous path for locomotion; gastrovascular cavity with mouth and proboscis; example, Planaria (Fig. 48).

Class 2, Trematoda (flukes).—Parasitic solitary flatworms; exterior nonciliated; mouth and digestive tract, but no proboscis; one or more suckers for attachment and feeding; nervous system degenerate; reproductive system very complex; complex life histories; example, liver fluke (Fig. 49, A).

Class 3, Cestoda (tapeworms).—Parasitic worms living in adult stages in intestines of vertebrates; form by strobilation extensive semipermanent chains of zoöids; no digestive tract; no mouth; nervous system degenerate; reproductive system elaborate; life cycle complex (Fig. 49, B).

FIG. 48.

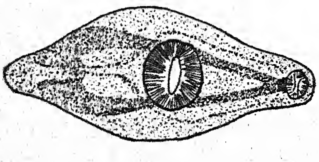


FIG. 49 A.

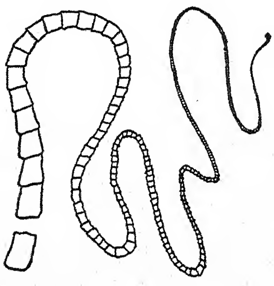


FIG. 49 B.

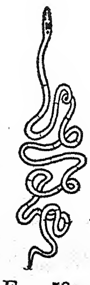


FIG. 50.

PHYLUM 4, NEMERTINEA.—An odd group of long, ribbonlike worms, which are nonparasitic; commonly classed as a division of Platyhelminthes, but they have an alimentary tract with mouth and anus and a distinct blood vascular system; no true cœlom; are characterized by a very long protrusible proboscis; forms of very uncertain relationships (Fig. 50).

PHYLUM 5, NEMATHELMINTHES (roundworms).—Elongated, cylindrical, unsegmented worms; digestive tract with mouth and anus; body cavity not a true cœlom, as it is not surrounded by mesoderm, but seems to act as a blood vascular system; some parasitic, but many free living; example, Ascaris (Fig. 51).

PHYLUM 6, ROTIFERA OR TROCHELMINTHES (wheel animalcules).—Minute aquatic triploblastic, bilaterally symmetrical forms, with cilia around the mouth that have a motion suggesting a rotating wheel; conspicuous masticatory apparatus in the pharynx; body cavity not a true cœlom, i.e., not lined with mesoderm (Fig. 52).

FIG. 51.

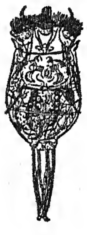


FIG. 52.

FIG. 53.

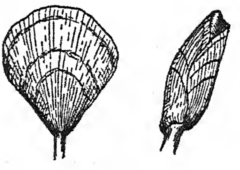


FIG. 54.

PHYLUM 7, BRYOZOA OR POLYZOA (moss animals).—Minute aquatic sessile animals; usually colonial; U-shaped digestive tract with mouth and anus close together; with a lophophore, a feathery food-collecting apparatus consisting of a horseshoe-shaped group of tentacles. Affinities very obscure, probably distantly related to Brachiopoda (Fig. 53).

PHYLUM 8, BRACHIOPODA (MOLLUSCOIDEA) (lamp shells).—Marine forms with a bivalve shell; usually attached by a stalk (peduncle); coiled lophophore with two spiral arms to right and

left of mouth; alimentary tract with mouth and anus; affinities very obscure, probably distantly related to Bryozoa (Fig. 54).

PHYLUM 9, ANNELIDA (segmented worms).—Bilaterally symmetrical worms; with internal and external metamerism; a true cœlom formed by hollowing out mesodermal cords; mouth and anus; closed blood vascular system; ventral nontubular nerve cord; nonjointed appendages; distinct trochophore larva.

Class 1, Archiannelida.—Marine worms without parapodia or setæ (Fig. 55).

Class 2, Chætopoda.—With setæ or bristles arranged in pits in the integument or on nonjointed appendages, parapodia (Fig. 56).

Class 3, Hirudinea (leeches).—Somewhat flat-bodied worms; without setæ; with suckers, one surrounding the mouth; body cavity filled with loose connective tissue; several external rings to each true metamere (Fig. 57).

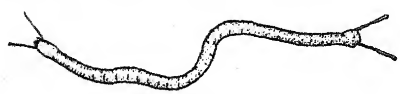


FIG. 55.

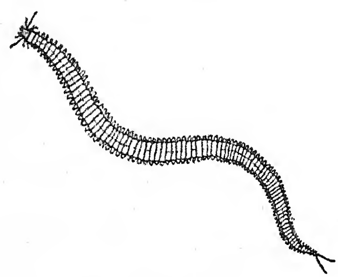


FIG. 56.

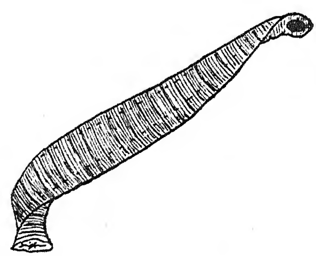
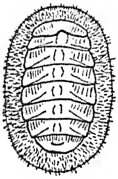


FIG. 57.

PHYLUM 10, MOLLUSCA.—Unsegmented; no jointed appendages; body divided into head, foot, and visceral mass; three pairs of ganglia, one pair for each of body parts; bilaterally symmetrical though secondarily asymmetrically coiled in gastropoda; open circulatory system; usually with a shell secreted by a mantle; mouth and anus; cœlom largely filled with blood sinuses and connective tissue.

Class 1, Amphineura.—Shows slight tendency toward metamerism, with eight linearly arranged shells or plates and linearly repeated gills (Fig. 58).



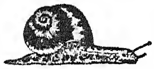
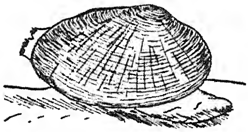


Fig. 59.



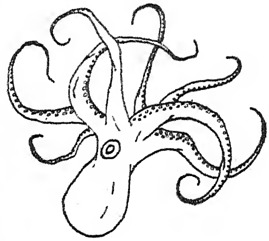


Fig. 58. Fig. 60. Fig. 61. Fig. 62.

Class 2, Gastropoda.—Usually with spirally coiled shell; well-developed head with tentacles; body, except head, coiled like the shell; foot flat (Fig. 59).

Class 3, Scaphopoda (toothshells).—Mantle and shell forming a tube about the body, with two openings, the anterior being larger; shell resembles a hollow tusk or tooth (Fig. 61).

Class 4, Pelecypoda (clams).—Headless forms with bilaterally symmetrical body and bivalve shell; the mantle is bilobed like shell; gills lamella-like, giving them the name Lamellibranchiata; foot is plowshare-like in shape (Fig. 60).

Class 5, Cephalopoda (squids, octopus).—Foot partly surrounds the head and is extended into tentacles on which are suckers; part of foot modified into siphon, which is used in locomotion; well-developed eyes and jaws, shell usually imbedded in mantle (Fig. 62).

Phylum 11, Arthropoda.—Paired, jointed appendages; metameric, with internal and external segmentation equally distinct; chitinous exoskeleton; ventral nontubular nerve cord; a six-segmented head; greatly reduced cœlom derived by hollowing out mesodermal cords; open circulatory system; strong tendency to concentrate and specialize metameres (heteronomous).

Class 1, Crustacea.—Mostly aquatic forms usually with gills; two pairs of antennæ; exoskeleton chitinous, but with lime mixed with it; examples, water fleas, crayfish, crabs, sow bugs, barnacles (Fig. 63).

Class 2, Onychophora (Peripatus).—A connecting-link group, with a combination of annelid and arthropod characters (Fig. 64).

Class 3, Myriapoda (centipedes and millipedes).—Elongate, somewhat wormlike arthropods, with numerous pairs of similar legs; one pair of antennæ; tracheæ; all terrestrial forms (Fig. 65).

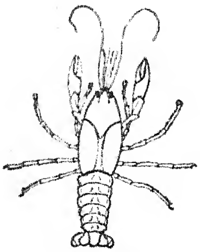


FIG. 63.

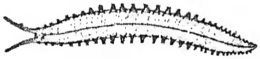


FIG. 64.

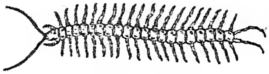


FIG. 65.

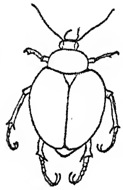


FIG. 66.

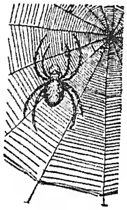


FIG. 67.

Class 4, Insecta (Hexapoda).—Six-legged; wings usually present; one pair of antennæ; tracheæ; mostly terrestrial, but a few secondarily aquatic; examples, grasshoppers, beetles, bugs, butterflies, bees, flies (Fig. 66).

Class 5, Arachnida.—Four pairs of legs; no antennae; breathe with tracheæ, lung-books, or gill-books; nearly all terrestrial; examples, spiders, scorpions, ticks, mites (Fig. 67).

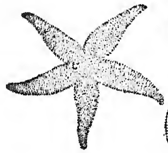
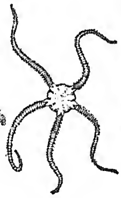
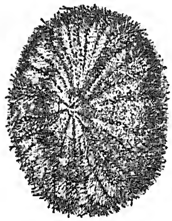
PHYLUM 12, ECHINODERMATA (Echinoderma).—Pseudoradially symmetrical adults, bilaterally symmetrical larvæ; skin usually spiny; large true cœlom formed by outpouching of archenteron; calcareous dermal plates; a peculiar water-vascular system used for locomotion and food capture; nonmetameric, though the larvæ show a tendency to be metameric in cœlomic pouches.

Class 1, Asteroidea (starfishes).—Usually five (or more) arms or rays, not distinctly marked off from central disk; distinct ambulacral groove in each ray; short skin spines; pedicellariæ; dermal branchiæ (Fig. 68).

Class 2, Ophiuroidea (brittle stars, serpent stars, basket stars).—Arms typically five, sometimes branched; arms sharply marked off from central disk; no ambulacral grooves (Fig. 69).

Class 3, Echinoidea (sea urchins).—Globular or flattened bodies without arms; a test or shell of continuous plates; long movable spines; comparable to starfish with aboral surface reduced and rays bent upward to meet at aboral pole; mouth with grinding apparatus (Aristotle's lantern); pedicellariæ (Fig. 70).

Class 4, Holothuroidea (sea cucumbers).—Body elongated in oral-aboral axis; soft bodied with reduced skeleton; body wall very muscular; some indication of bilateral symmetry in adult (Fig. 71).

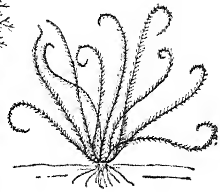


FIG. 68. FIG. 69. FIG. 70. FIG. 71. FIG. 72.

Class 5, Crinoidea (sea lilies, feather stars).—Usually sessile (a few only temporarily so), fastened to a stalk at aboral pole; five arms generally much branched; largely extinct, but represented by a few modern Families (Fig. 72).

PHYLUM 13, CHORDATA.—Notochord at least in embryos; gill slits (pharyngeal clefts); dorsal, tubular central nervous system; true cœlom, derived by outpouching of archenteron; metameric, but segmentation confined largely to internal structures and arrived at in an entirely different way from that in annelids and arthropods; closed circulatory system; bilaterally symmetrical; no more than two pairs of appendages, at least in modern forms.

Subphylum I, Hemichordata (Enteropneusta).—A group of wormlike and sessile forms in which certain structures have been doubtfully homologized with notochord, gill slits, and dorsal nerve cord of true chordates. Relationships uncertain, but they probably are distant relatives of chordates, echinoderms, and possibly nemerteans; examples, acorn worms (Fig. 73).

Subphylum II, Urochordata (Tunicata).—Marine forms in which the adult is typically a degenerate sessile type (free living in salpians and Larvacea); surrounded by a test or tunic; an atrium with atriopore; the larva a tadpole-like type with well-developed notochord in the tail (lost in adult); numerous gill slits in adult; examples, sea squirts (Fig. 74).

Subphylum III, Cephalochordata (Amphioxus).—Small fish-like chordates, with somewhat sedentary habit; notochord extending from end to end; numerous gill slits (50 or over); brain greatly reduced (acephalic); no appendages; atrium and atriopore (Fig. 75).

Subphylum IV, Craniata (Vertebrata).—Brain case (cranium) more or less developed; vertebræ more or less developed; brain

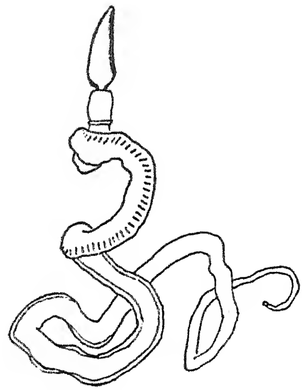


FIG. 73.

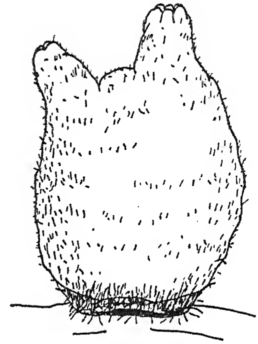


FIG. 74.

FIG. 75.

well-developed; no atrium or atriopore; complex system of endocrine glands; relatively few gill slits (14 in some cyclostomes, but rarely more than 6).

Class 1, Cyclostomata (lampreys and hagfishes).—Jawless, limbless vertebrates; with poorly developed cranium and vertebræ, persistent notochord (Fig. 76).

Class 2, Chondrichthyes (sharks, etc.).—Marine fishes with cartilaginous skeleton, no swim-bladder; hinged jaws; paired limbs; no true exoskeleton, but skin provided with dermal dentacles; upper jaws not firmly attached to the floor of the skull (Fig. 77).

Class 3, Osteichthyes (bony fishes).—Fresh-water and marine fishes with bony skeleton composed partly of ossified cartilage and partly of dermal scales that have sunk in and fused with the cartilage bones; a swim-bladder (lung); upper jaw fused to the base of the skull (Fig. 78).

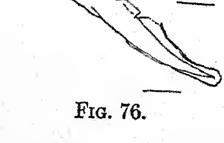


FIG. 76.

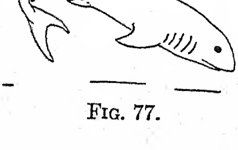


FIG. 77.

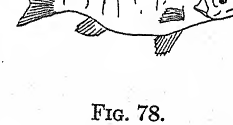


FIG. 78.

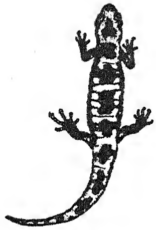


FIG. 79.

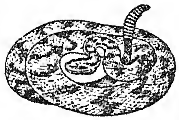


FIG. 80.

FIG. 81.

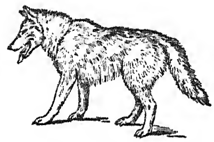


FIG. 82.

Class 4, Amphibia.—Usually terrestrial as adults, but aquatic as larvæ; legs instead of paired fins; lungs in adults, but gills usually in larvæ; three-chambered heart; examples, newts, salamanders, frogs (Fig. 79).

Class 5, Reptilia.—A "land egg" with shell, amnion, and allantois; no aquatic larvæ; no gills at any time; three-chambered heart (almost four-chambered in some); cold-blooded; toes with claws; examples, crocodiles, turtles, lizards, and snakes (Fig. 80).

Class 6, Aves (birds).—Mostly flying vertebrates with feathered wings; a beak (no teeth) in modern forms; bipedal; warm-blooded; four-chambered heart; "land egg" with shell, amnion, and allantois as in reptiles (Fig. 81).

Class 7, Mammalia (mammals).—Suckle young with mammary glands, possess hair; usually give birth to living young (but some primitive forms lay reptile-like eggs); four-chambered heart, warm-blooded; mostly quadrupedal; a diaphragm separates body cavity into abdominal and chest cavities; examples, dogs, mice, cattle, monkeys, man (Fig. 82).

C. Discussion of the Probable Interrelationships of the Animal Phyla

The problem of the phylogenetic (ancestral) relationships of the various animal Phyla to one another received a great deal of attention from morphologists of the older schools, but during the last few decades the experimental method has come so to dominate biological science that the somewhat speculative phylogenetic aspects of the science have grown into disrepute. Of late, however, interest in phylogeny has been revived in various parts of the world, especially in connection with one of our great seaside

laboratories, where a group of American zoölogists has collaborated in working out a new theory of phyletic relationships that has come to be known as the theory of the DIPHYLETIC TREE, a diagrammatic expression of which is shown in Figure 83.

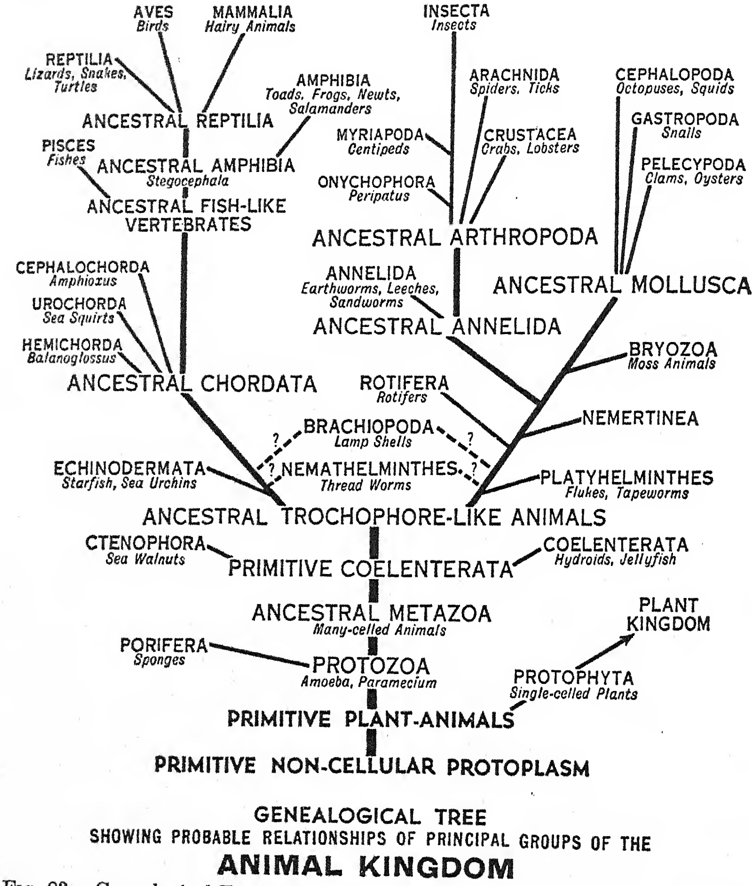


FIG. 83. Genealogical Tree of the Animal Kingdom. (Designed by Sigerfoos after Allee.)

This theory is coming to be rather widely accepted as the best supported guess as to the broader lines of animal relationship, but must not be accepted as more than tentative at the present time. Uncertain as it is in some of its details, it has great pedagogical value in that it helps to unify and correlate our knowledge

of animal morphology, and especially of those very general characteristics of organisms that form the bases for classification of animals into their larger groupings.

To give an adequate presentation of the evidences upon which the theory is based would not only require more pages than we can spare, but would involve us in a technical discussion of many matters that would be quite unintelligible to beginning students. Since, however, we propose to present the representatives of the various Phyla in the order suggested by the diphyletic system of descent, it seems necessary to attempt a brief and simplified justification of the diphyletic tree.

1. *The Simpler Forms*

a. The Primitive Plant-Animals.—At the bottom of the tree we find an anomalous group of lowly organisms, unicellular in character and possessed of a combination of plant and animal characters. In this group we would place the slime molds and such forms as Euglena, Volvox, and others that are claimed by both botanists and zoölogists.

b. The Protozoa.—From the plant-animals it is believed that two main branches arose, the PROTOPHYTA (unicellular plants) and PROTOZOA (unicellular animals). From these two main trunks arose the Animal and the Plant Kingdoms. Since this is a course in Zoölogy, we shall confine our attention to the Animal Kingdom. At the bottom of the main animal trunk are the Protozoa, many representatives of which are still surviving in the primitive form so far as their unicellular character is concerned. The ancestral Protozoa are believed to have undergone divergence into two distinct subkingdoms, modern PROTOZOA and METAZOA. The Protozoa have retained the one-celled structure characteristic of the earliest forms of life and have proceeded to specialize parts of the single cell for various functions. The Metazoa have adopted the scheme of multicellularity, involving specialization of groups of cells for a great variety of functions. Hence the Protozoa might be called CELL ANIMALS and the Metazoa TISSUE ANIMALS.

c. The Porifera (**Sponges**).—This group is multicellular with a relatively slight degree of cellular differentiation and a poorly defined axiate organization. They are viewed as an unprogressive side line of evolution that has led to no other groups than to the sponges themselves, the least animated of present-day animals.

Because they seem to have no affinities to any other Metazoa, the Porifera may be considered as a third independent offshoot of the primitive protozoan stock correlative with the Protozoa and the Metazoa. They are placed in a separate Division, called PARAZOA.

d. The Cœlenterata.—Constituting the first really progressive metazoan stock and generally recognized as belonging at the base of the main trunk of metazoan evolution, and thus the ancestral to all higher groups, are the Cœlenterata. The cœlenterates are the only DIPLOBLASTIC true Metazoa now living and are also the only Metazoa that exhibit no extensive bilateral symmetry, but are primitively radially symmetrical.

2. *The Basis for the Diphyletic System*

Above the cœlenterate level the diphyletic system begins, for all the other phyla, with a few doubtful exceptions, may be arranged in the form of two main branches each subdividing into a number of minor branches. The right-hand branch in our diagram (Fig. 83) contains the majority of metazoan Phyla and is called for convenience the ANNELID-ARTHROPOD BRANCH; the left branch includes only a few Phyla and is called the ECHINODERM-CHORDATE BRANCH. The series of forms making up the two great branches have many fundamental features in common among the members of the same branch, and many differences between the members of different branches. Some of the *criteria upon which the diphyletic arrangement rests* may be briefly outlined as follows:—

a. Determinate and Indeterminate Cleavage.—The members of the Annelid-arthropod series exhibit typically a mode of cleavage (the early divisions of the egg leading to embryo formation) known as DETERMINATE. In this type of cleavage the blastomeres, or early embryonic cells, are very definitely arranged in a stereotyped pattern and each early cell has a fixed prospective rôle in the formation of a particular part of the body. The members of the Echinoderm-chordate series, on the other hand, exhibit typically a mode of cleavage known as INDETERMINATE, in which the cleavage pattern lacks definiteness and the early blastomeres retain their unspecialized character and whose fate in tissue formation is still undetermined. There are several important exceptions to this rule that will readily occur to any zoölogist, but there are explanations for these that cannot be presented with-

out too serious a digression. This is on the whole the poorest of the four criteria listed.

b. Methods of Mesoderm Formation.—In the members of the Annelid-arthropod series the mesoderm (third germ layer) arises from one particular cleavage cell designated by students of cell lineage as "4D." This cell gives rise by division to two pole cells from which two solid mesodermic bands, a right and a left, proliferate. In the Echinoderm-chordate series the mesoderm arises in an entirely different fashion, as out-pouchings of an already well-defined embryonic tissue, the primitive gut, or archenteron.

c. Methods of Cœlom Formation.—In the Annelid-arthropod series the cœlom, or true body cavity, arises by a secondary hollowing out of the originally solid mesodermal bands, the cells merely spreading apart so as to produce a cavity or series of paired cavities. In the Echinoderm-chordate series the cœlom is formed by means of paired out-pouchings of the archenteron, or primitive gut. In these the cavity is present from the first and was once continuous with the archenteric cavity.

d. Mouth Formation.—In the Annelid-arthropod series the blastopore, or primitive mouth, of the blastula (the two-layered embryonic stage) gives rise directly to the true mouth of later stages and an anus is secondarily opened up at the opposite end. In the Echinoderm-chordate series the primitive mouth of the blastula becomes the anus of later stages and a new mouth is opened up by secondary processes.

All of these criteria represent morphologic characters of a very deep-seated and fundamental sort, about the most fundamental that could well be found. Taken together they afford a firmer foundation for phylogenetic theory than we have had heretofore.

3. *General Statement about the Annelid-Arthropod Assemblage*

We are not to think of the members of this series as in any sense a linear phylogenetic series, each higher type being a descendant of the type next lower in the series. Rather, it seems more likely that they all represent side branches from some as yet unknown ancestral stem that gave rise at different levels to the ancestors of the present-day Phyla. A hypothetical "trochozoan" common ancestor has been suggested, a type resembling in some respects the trochophore larvæ of the various Phyla and in other respects the adult ctenophores of today. Among the upper Phyla of this

series there is evidence of much more direct descent. Connecting-link types, both living and fossil, help to bridge the gaps between the annelids and the arthropods and between the various arthropod Classes.

4. *General Statement about the Echinoderm-Chordate Assemblage*

The left-hand branch of the tree contains relatively few Phyla, but must not be neglected, for this is the branch that has given rise to the vertebrates, including man. The series includes the roundworms, the arrow worms, the echinoderms, the various Subphyla of chordates, and the true vertebrates. There is some question as to the correctness of this placing of the roundworms. At best they must be viewed as an early aberrant side branch that has been relatively unprogressive in structure, but extraordinarily successful in exploiting the earth. The affinities between the echinoderms and the chordates, and between the latter and the vertebrates, are unmistakable. It is thought that the main stem ancestral type must have resembled in many respects the larvæ of certain types of echinoderms and chordates. There is, for example, a striking resemblance between the larva of the primitive chordate, Balanoglossus, and those of such echinoderms as the starfishes and sea cucumbers. In several other important respects the echinoderms and the chordates show resemblances, but these are of too technical a nature to be presented at this time. It would seem to be more in accord with the facts to place the brachiopods and roundworms on separate branches independent of the two main branches.

5. *Other Theories of Interphylum Relationships*

Several other views more or less in general accord with the Diphyletic Tree concept are held by zoölogists. My colleague Professor Emerson, for example, is inclined to carry the main trunk of the "tree" several stages above the cœlenterates, putting the Ctenophora, the Platyhelminthes, and the Nemerteans as lateral branches of the main trunk below the point of its branching into the annelid-arthropod and echinoderm-chordate branches. His reason for this is his feeling that mesoderm formation and bilateral symmetry, especially the latter, occurred only once and appeared before the two main branches diverged. It seems quite reasonable, however, to believe that convergent evolution with

respect to both of these important characters may have occurred in two or more independent stocks. This is highly probable, for mesoderm formation in flatworms is like that in the annelid-arthropod group and is entirely different from that in the chordate-echinoderm group. The idea that the flatworms belong to the main trunk would imply that their alleged descendants in the echinoderm-arthropod branch gave up one mode of mesoderm formation and developed another quite different one.

Many biologists have been inclined to consider that the annelids belong to the main trunk of the "tree" and that they diverged into chordates on the one hand and arthropods on the other. The main reason for this view is that it is assumed that metamerism occurred only once and that all higher metameric forms must therefore have been derived from the lowest metameric group. This view, however, is hardly tenable at this time, for it is rather generally recognized that, although metamerism in annelids is homologous with that in arthropods, it is not at all homologous with that of vertebrates. On the whole, then, these modifications of the diphyletic tree are not as readily accepted as the original diphyletic concept of Allee and others.

Another view, one with which the writer sympathizes, is that, while the majority of the important Phyla submit to arrangement into a diphyletic grouping, several Phyla such as roundworms, brachiopods, arrow worms, and Polyzoa, do not fit such a simple scheme. Would it not be better to assume that they represent several independent lines of evolution or independent small branches coming off from the cœlenterate stock at about the same time that the two more successful branches came off?

The most radical view of interphylum relations is the so-called polyphyletic concept, according to which each of the Phyla, or at least several groups of them, came off independently from a protozoan level. According to this view, such features as are common to all or many of the present Phyla (bilaterality, mesoderm, cœlom, blood circulation, etc.) have been the product of convergent evolution i.e., have developed independently in several groups because of common environmental stimuli. This last view is the least acceptable of all those given.

The reader will realize that phylogeny, the science of ancestral relations, when applied to different Phyla is a hazardous pursuit. It is interesting to speculate about such distant relationships—

and all thorough-going zoölogists find themselves driven to speculate about these matters—but one must admit that the result is largely hypothetical. We shall therefore take it only for what it is worth, as interesting speculation and no more.

SUMMARY

1. The synoptic classification given in this chapter is merely for purposes of obtaining a bird's-eye-view of the Animal Kingdom before beginning the study of the types.

2. The diphyletic tree is a schematic arrangement of animal Phyla indicating the views of some zoölogists as to the phylogenetic relationships of the various Phyla. This scheme is highly theoretical and should be regarded as tentative.

3. The relationships shown in the tree are based upon fundamental resemblances and differences in embryonic characters: mode of cleavage, methods of mesoderm formation, methods of cœlom formation, and the relations of mouth and anus to the blastopore.

4. Other theories of interphylum relationships differ in some details from the one presented, but only one of them, the polyphyletic theory, differs greatly from the diphyletic scheme.

NOTE. Figures 37 to 82 are intended to give the student merely a general idea of the external appearance of the main kinds of animals that constitute the Animal Kingdom. Names of the species shown in the figures are omitted in order that the section on classification may not be overburdened with new terms. These figures have either been drawn from original materials or borrowed from other publications. Through the kindness of the General Biological Supply House Figures 41, 43, 44, 46, 47, 54, 55, 68, 69, and 79 have been borrowed from their *Red Book*. Figures 50, 51, 52, 53, 61, and 70 have been borrowed from Hegner's *Invertebrate Zoölogy*. Figures 80, 81, and 82 have come from Newman's *Vertebrate Zoölogy*. The remainder have been drawn for the purpose by Mrs. Katherine McClure Roehl, who until recently had charge of the teaching of Zoölogy in the Port Huron Junior College. Mrs. Roehl has also collaborated with the writer in the production of a laboratory manual to accompany this text.

PART III

REPRESENTATIVE ANIMAL TYPES
(INVERTEBRATES)

CHAPTER XIV

THE SUBKINGDOM PROTOZOA

A. Protozoa Defined and Characterized

Protozoa have been defined as organisms consisting of one cell, while Metazoa are organisms consisting of many cells. It is implied that we mean the same thing by the word "cell" in both cases. The whole protozoan individual is supposed to be essentially equivalent to any single cell of a metazoan organism except that the latter may be specialized in many ways for particular functions, while the former has retained the primitive versatility of ancestral cells and is therefore able to perform all the necessary vital functions. Out of this conception of the Protozoa the conviction has grown that they are essentially extremely simple animals without special organs for special functions, and that the undifferentiated protoplasm performs all functions. This interpretation of the Protozoa is the logical result of a too slavish adherence to the Cell Theory: the idea that a cell is a cell wherever one finds it and that a protozoan is merely an independent cell. This conception of the Protozoa is misleading and needs to be contrasted sharply with the organismal view of this group.

First and foremost, a protozoan is an organism. That it is an organism without divisions into separate cells is an important consideration, but it is not paramount. ***Clifford Dobell,*** the eminent English protozoölogist, expresses the most radical antagonism to the interpretation of Protozoa as one-celled animals when he says that the protozoan body "does not correspond to a minute fragment of a metazoan body, one of its myriads of cells, but to the whole body." Dobell's distinction between the Protozoa and the Metazoa is expressed in the idea that the latter are CELLULAR, the former NONCELLULAR.

According to this conception the metazoan is an organism which has made use of the scheme of dividing up its nucleus and cytoplasm into a large number of units (cells) the more effectively to accomplish differentiation into organs and tissues specialized for particular functions. The protozoan is likewise a complete organ-

ism which has been able to attain various degrees of complexity of organization and specialization of function without resort to the cellular scheme. Protozoa have in many cases great complexity of organization. Organs of all sorts are to be found within the limits of the protozoan body, but they are not composed of tissues or cells in the sense of the Cell Theory.

On the other side of this controversy it must be said that a protozoan usually has but one nucleus; that this nucleus contains chromatin; that distinct chromosomes may often be distinguished; that nuclei divide by a process very similar to mitotic cell division; and that the whole protozoan body is divided much as a single cell is divided. Moreover, whole protozoans are differentiated into gametes, equivalent to egg cells or sperm cells in the Metazoa, and the sperm individuals fuse with the egg individuals in a fashion that is unmistakably equivalent to fertilization. Not only this, but prior to their union the prospective gametes appear to undergo reduction divisions similar to those exhibited by eggs and sperm cells during maturation. This and much more evidence points strongly to the conclusion that protozoans are cells and that the whole individual protozoan is in a sense equivalent to a germ cell or any other cell of a metazoan organism. Dobell's radical suggestion that Protozoa be regarded as noncellular organisms is, therefore, not likely to gain general acceptance. Yet he has done good service in pointing out that a too slavish adherence to the implications of the Cell Theory has caused the Protozoa to be wrongly interpreted. With Professor Ritter, we may conclude that in connection with the Protozoa "the concept *cell* must be held in strict subordination to the concept *organism,* in this as well as in other portions of the living world." The protozoan is unquestionably a cell, but it is more than that: it is a complete organism.

B. The False Idea of the Simplicity of Protozoa

Because a protozoan is a single cell, an impression has come to prevail that it is on that account relatively simple. "Hardly anything," says ***Ritter,*** "could be more misleading than the almost universal practice in elementary teaching of introducing beginners to the Protozoa by showing, very superficially, an Amœba and emphasizing its simplicity, and then keeping it in the foreground of the learner's thought as an exemplification of the doctrine that

the Protozoa are 'extremely simple' animals, that they are undifferentiated into organs and tissues—that in fact they are hardly 'true animals at all.'" No better method of correcting this misapprehension is available than to compare a highly differentiated protozoan with one of the simpler metazoans. For this purpose

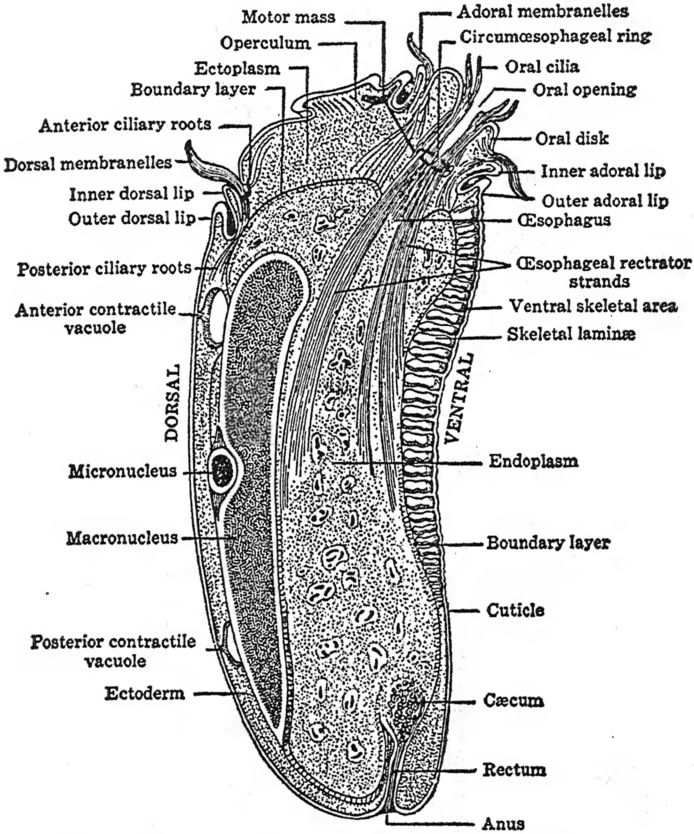


FIG. 84. *Diplodinium ecaudatum.* An example of a complex protozoan. (After Sharp.)

let us compare *Diplodinium ecaudatum* (Fig. 84)—a ciliate protozoan which inhabits the intestine of cattle—with a fresh-water Hydra (Fig. 85). Both figures are longitudinal sections showing the amount of differentiation present. Which is the more complex, and which the simpler organism? One basis for comparison of the

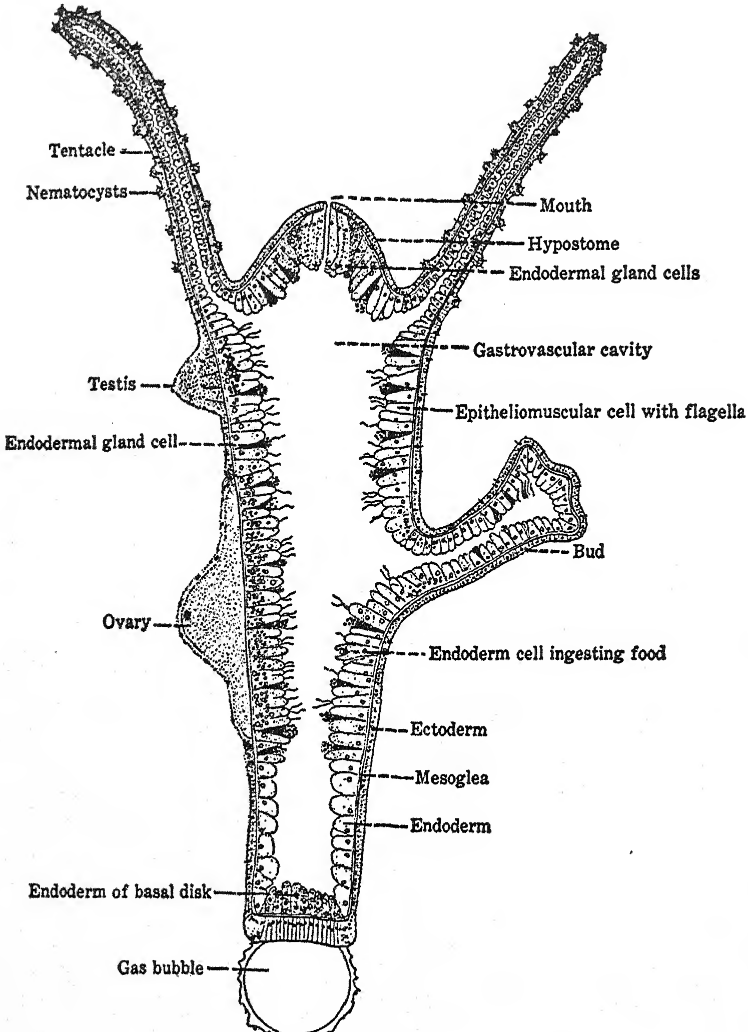


FIG. 85. *Hydra.* An example of a simple metazoan. (From Hegner, after Kepner and Miller.)

degrees of differentiation present is to count the labeled regions in the two. There are 33 labeled structures, all of them different, in the protozoan, Diplodinium, and only 16 different labeled structures in the metazoan, Hydra.

Objections have been made to this mode of comparison on the ground that, were Hydra magnified to the same degree as Diplodinium, many more differentiated structures would be revealed, and that if these were all labeled, Hydra would then appear the more complex of the two. In spite of these considerations Ritter seems to the writer to be more or less justified in his claim that Diplodinium, a microscopic protozoan organism, is more highly differentiated than the much larger metazoan, Hydra. It has a skeleton, a digestive tract with mouth and anus, locomotor organs, excretory organs, contractile organs performing a muscular function, sensory, and conductile organs. This organism gives one a good idea of what may be attained in complexity of organization without employing the scheme of multicellularity and of cellular specialization. The animal has a definite organization, with organs of higher rates of metabolism situated at the anterior end and those of lower rates of metabolism at the posterior end. We find regions of the cytoplasm clearly differentiated into organs or systems. Even a nervous system is present consisting of receptors and effectors, the latter associated with muscular organs. We call these structures ORGANS (more technically, ORGANELLES), and advisedly so, for we cannot exclude them from such a title unless we arbitrarily define organs so as to include only structures composed of many cells.

Only the small size of Diplodinium prevents the general recognition that it is a relatively highly differentiated organism. Too readily we assume its lowly status because it is a protozoan. There are simple Protozoa and there are complex Protozoa—just as there are both simple and complex Metazoa—and there is about as wide a divergence between simplest and most complex within the bounds of one Subkingdom as within those of the other. In neither group are there forms that very closely approach real simplicity of organization approximating a homogeneous or structureless condition. A baseless assumption that some Protozoa are essentially undifferentiated masses of protoplasm has found its way into the more speculative phases of biological literature. A good illustration of the fallacy is found in *Haeckel's The Evolution*

of Man, where he says: "The earliest unicellular organisms can only have been evolved from the simplest organisms we know, the *monera*. These are the simplest living things we can conceive. Their whole body is nothing but a particle of plasm, a granule of albuminous matter." As a matter of fact this *monera* is a pure fiction. There are no Protozoa that even approximate the condition of an undifferentiated, unorganized particle of plasm.

We shall next make a detailed examination of *Amœba proteus* as a type of the less complex Protozoa and of *Paramecium caudatum* as an example of the more complex Protozoa. From these two studies we may gain a general knowledge of the biology of the group.

SUMMARY

1. Protozoa are defined as organisms in which the whole individual, though it may exhibit a high degree of specialization of parts, is in a sense a single cell.
2. Dobell defines Protozoa as noncellular and Metazoa as cellular organisms.
3. A discussion is given of the Cell Theory as applied to Protozoa.
4. Some of the Protozoa prove on study to be extraordinarily complex, contradicting the idea that they are very simple animals. Ritter claims that in degree of complexity the protozoan, Diplodinium, compares favorably with the metazoan, Hydra.

CHAPTER XV

AMŒBA
(SUBKINGDOM PROTOZOA)

No microscopic organism has come to be an object of so general popular interest as Amœba. Even writers of fiction speak glibly of the course of evolution "from Amœba to man." One popular writer refers to Amœba as "the Adam and Eve of animate life." The impression prevails that Amœba is the lowest possible expression of life, a mere primordial mass of substance endowed with a spark of life. Not only is Amœba supposed to occupy the lowest rung of the phylogenetic ladder, but the assertion is not infrequently made that it is the actual ancestor of higher forms of life. The absurdity of claiming a relationship of ancestry and posterity between two contemporaneous groups need scarcely be pointed out, but this is the same fallacy as that involved in statements that man is the descendant of the present anthropoid apes or monkeys. Amœba is supposed to be a lowly form of life that has lived and multiplied throughout the millions of years since life began without having very materially advanced. The pedigree of Amœba is doubtless as long as that of man and involves hundreds of times as many generations, yet Amœba remains in a relatively primitive and uncomplicated state. It may possibly have had a period of greater complexity of organization and then regressed secondarily to a simpler condition. About the real ancestral history of Amœba we know nothing.

A. General Characters of Amœba Proteus

There are many kinds (species) of Amœba, some simpler, some more complex than *Amœba proteus*. Hence the species which we are going to study in detail is a sort of representative Amœba. This little organism, sometimes called the "proteus animalcule," when in the full-grown state is about .25 mm. ($\frac{1}{100}$ of an inch) in diameter, a relatively large one-celled organism. It lives in fresh-water ponds and in damp places. ***Leidy,*** who published a classic study of Amœba and its relatives, found his best specimens in

some abandoned tanning pits. *Amœba proteus* was doubtless named after Proteus, a mythological sea god of the ancients, who was constantly changing his shape. Its ever shifting form is a characteristic of Amœba: its irregular outlines are always changing. It is often described as a shapeless mass of protoplasm, colorless except for the presence of darker food particles inclosed within its substance. Careful examination and study of its behavior indicate, however, that it is a true organism and that it is less simple than some would have us believe. ***Hyman*** has shown experimentally that Amœba has a definite though shifting axiate organization. There is always, in an active individual, one end that keeps ahead in locomotion and an opposite end that drags behind. Lobe-like PSEUDOPODIA are thrust out in the direction of locomotion and the latest pseudopod represents for the time being the controlling region, or the apical end, of Amœba. A newer pseudopod then usurps control and the older ones retire to subordinate rank and withdraw. Amœba then has an organization, but one that is not fixed for long periods, a shifting organization which is to be contrasted sharply with that of Paramecium.

B. General Anatomy of Amœba Proteus

It is customary to distinguish in the body of Amœba two main structural regions: an outer clear, translucent layer of apparently homogeneous protoplasm, the ECTOPLASM, and an inner, central mass of heterogeneous consistency, the ENDOPLASM (Fig. 86, **C**). Somewhere in the endoplasm lies a NUCLEUS, and, moving about more or less, a CONTRACTILE VACUOLE which disappears and reappears at intervals. Numerous vacuoles containing particles of food in various stages of digestion lie scattered about the endoplasm. Occasionally one of these FOOD VACUOLES, containing débris consisting of sand grains or indigestible food materials, approaches the exterior, breaks through the ectoplasm, and discharges its contents (Fig. 86, **A**). Each of these regions and organs demands more detailed examination.

The ECTOPLASM (ec) is not a true cell membrane, but possesses at least the functional equivalent of a membrane on its outer surface; in fact, a distinct PELLICLE has been demonstrated by microdissection methods in *Amœba verrucosa*. The whole ectoplasm has a semisolid or gelatinous consistency and is able to change shape only quite slowly.

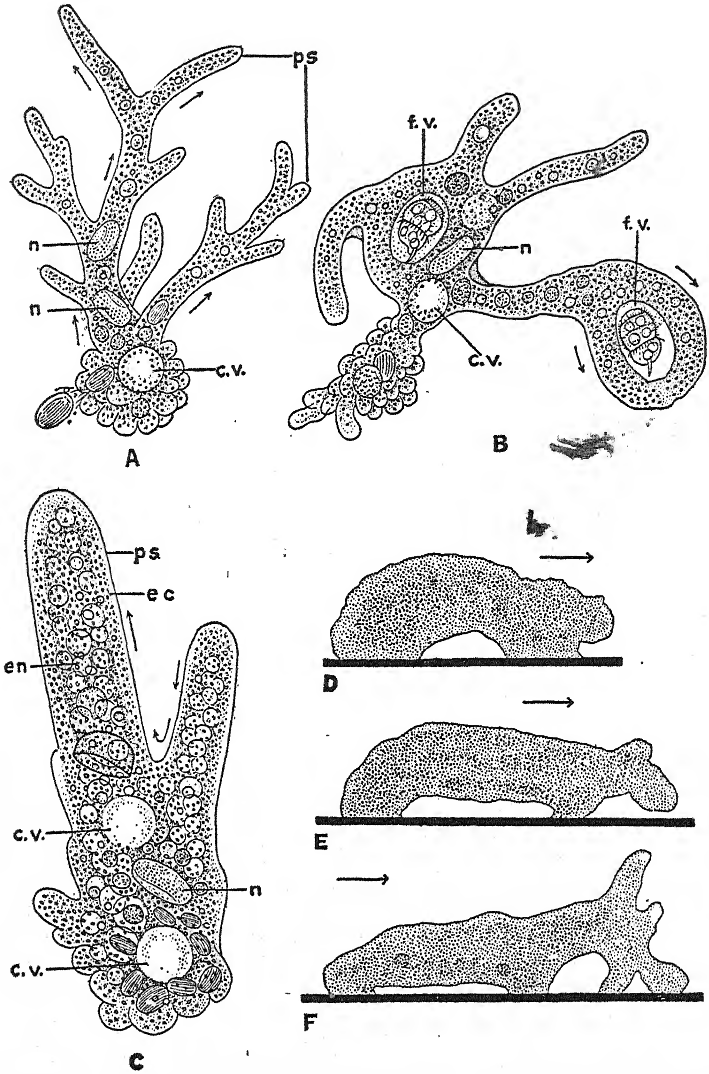


FIG. 86. *Amœba proteus*. A, B, C, various forms assumed by this species. c.v., contractile vacuoles; ec, ectoplasm; en, endoplasm; f.v., food vacuoles containing other organisms in process of digestion; n, nucleus; ps, pseudopodium. Arrows indicate the direction of the movement of the pseudopodia. D, E, F, show three successive views of a single Amœba walking; arrows show direction of progress. In D a new pseudopod is extending; in E this is about to attach itself to the substratum and a second pseudopod is forming; in F both first and second pseudopods have attached themselves, and two new pseudopods are forming. (A, B, C, after Leidy; D, E, F, after Dellinger.)

The ENDOPLASM (en) is much more fluid in its consistency. One can readily see vesicles shifting about as though suspended in a fluid medium. The two body regions are not sharply marked off from each other but seem to blend one into the other.

The NUCLEUS (n) is so nearly colorless and so likely to be surrounded by other, more visible granules and vacuoles that it is difficult to distinguish in living specimens. In stained and mounted specimens, however, it is seen to have the form of a somewhat flattened sphere whose position with reference to the other structures of the body is quite variable. It has a definite nuclear membrane and contains a large number of small deeply staining, spherical particles that have all the properties of CHROMATIN. The nucleus has been shown experimentally to be the metabolic center of the body. If a large Amœba be cut into two pieces, one with the nucleus and the other without, the nucleated piece lives on normally, grows, and multiplies; while the enucleated piece ceases to feed or to grow and soon wastes away and dies. The nucleus plays also a very important rôle in reproduction, as will be brought out in a subsequent paragraph.

The CONTRACTILE VACUOLE (c.v.) can be seen under the microscope as a clear round space, slightly pinkish in tint and larger than other vesicular bodies in the endoplasm, which arises as a small spot and then grows larger and larger until, like a bubble from a bubble pipe, it bursts and disappears. This body, judging by its optical properties, is a vesicle filled with watery fluid which is collected from the surrounding protoplasm and then discharged through a perforation in the ectoplasm. Careful studies of the phases of growth and discharge of this structure have shown that the vacuole first lies near the nucleus, but as it grows it leaves the latter and moves toward the surface, coming to rest against the ectoplasm near the posterior end of the body. It presses against the ectoplasm, flattening it out until only a thin film separates it from the exterior. This film finally breaks suddenly and the contents of the vacuole are discharged. The function of the contractile vacuole is not fully determined, but the consensus of opinion is that it serves as a means of regulating the proportion of water in the body of the organism. Feeding processes seem to require the taking in of a good deal more water than can be used, and excess water must be eliminated. Recent work on Paramecium seems to indicate that the contractile vacuole excretes little, if

any, nitrogenous wastes. In view of this it is an open question whether in Amœba the contractile vacuole plays any other than a water regulating rôle.

C. Physiology of Amœba

1. *The Nutritive Process*

Amœba illustrates the processes of feeding, digestion, assimilation, energy production, and excretion, reduced to very simple terms. Thus we may study the whole metabolic cycle carried on within the confines of a small one-celled body. Amœba, like any other animal, depends for its nutriment upon smaller animals and

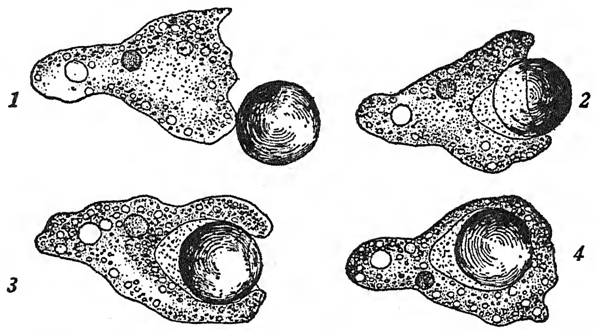


Fig. 87. Amœba ingesting a *Euglena* cyst. *1, 2, 3, 4,* successive stages in the process. (From Jennings.)

plants. Though so small and so lowly, it is a miniature pond ogre, going about seeking whom it may devour. Its prey consists chiefly of smaller Protozoa and small aquatic plants, such as desmids and diatoms. Even small Metazoa, such as rotifers, are caught, subdued, and swallowed whole by a large Amœba. An Amœba has the ability to discriminate between inorganic particles, such as sand, and objects suitable for food, and seems to show a preference for certain large species of diatoms, one of which is quite a meal for a protozoan.

a. How Amœba Feeds.—The taking of food into the body is called INGESTION and the mouth is the usual organ of ingestion. Amœba, curiously enough, has no mouth. Any point on the surface that comes into contact with food may become, for the time being, a mouth. The method of ingestion is that of engulfing (Fig. 86, B and Fig. 87). An Amœba in its forward progress comes in

contact with a food mass. The part immediately in contact with the food stops flowing forward and the parts of the body above, below, and on the sides, flow forward, forming a pocket about the food. The edges of the pocket bend in, meet, and fuse so as completely to surround the ingested object. More or less water is taken in at the same time and thus is formed a FOOD VACUOLE (Fig. 86, B and Fig. 87, *4*). One favorite kind of Amœba food is a filamentous green alga (Oscillaria), a primitive and very abundant water plant. Filaments many times the length of the Amœba are engulfed (Fig. 88). Starting in either at one end or the middle,

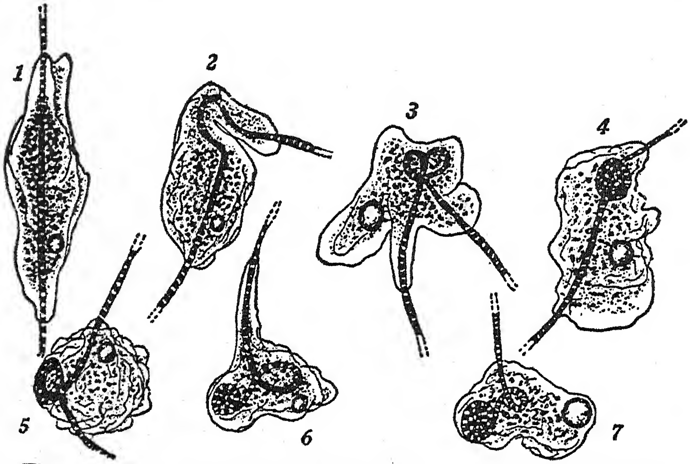


FIG. 88. *Amœba verrucosa*, showing stages (*1* to *7*) in devouring a filament of *Oscillaria*. (From Rhumbler.)

the ingested part is progressively coiled up inside until the protoplasm has flowed around the whole piece. Sometimes the prospective meal of an Amœba proves somewhat refractory, moving away when the process of engulfment begins, or struggling to release itself; but the devourer is not easily discouraged, following up and repeating its attempts until ultimately successful, or until the prey moves entirely out of range. Discrimination between inedible and edible substances implies sensibilities of a highly specific sort. Though there are no organs of smell or of taste, the surface protoplasm has the capacity to receive and to react to chemical and physical stimuli. In order properly to stimulate the engulfing act, a substance must have a certain amount of solidity and also certain chemical properties. Neither digestible

substances in solution nor nonnutritious solid particles are effective in stimulating the events of ingestion.

b. How Amœba Digests Its Food.—A food vacuole is in reality one of the stomachs of an Amœba in which its food is digested. It is more than a stomach; it is a whole digestive tract in miniature. The surrounding protoplasm secretes digestive juices and pours them into the vacuole. Food is rendered liquid and diffuses out of the vacuole into the surrounding protoplasm and the indigestible débris is carried to the surface and egested or cast out by being simply left behind when the Amœba moves on (Fig. 86, **A**); at least that is how it appears. A sort of baglike mass of heavy materials seems to gravitate toward the posterior end of a forward moving Amœba and when it becomes too heavy it seems to be merely dropped out through the ectoplasm, and the lightened organism moves on.

The whole process of metabolism seems to be about the same in Amœba as elsewhere: the dissolved food materials, such as sugars and amino-acids, are built up into living protoplasm and the living protoplasm is constantly breaking down by oxidative processes, releasing heat and energy for locomotion and other physiological activities. There is some evidence that the by-products of catabolism are the same as in larger animals, namely, water, urea, and CO_2.

c. How Amœba Breathes.—There is no question but that Amœba respires: it takes oxygen from the surrounding water and combines it with protoplasmic matter. Carbon dioxide and other wastes are given off either from the surface or by the contractile vacuoles. If an Amœba is placed in water from which oxygen has been removed, its activities gradually cease. No more food is ingested and it goes into a dormant condition from which it may be aroused by adding oxygen to the water. Amœbæ live commonly in rather foul water in which the amount of oxygen in solution is relatively low, and where, owing to the prevalence of decaying vegetation, the concentration of CO_2 is relatively high. Removal of oxygen from the water is therefore not immediately felt and it may take a number of hours to make an Amœba show marked signs of asphyxiation.

2. *The Locomotor Processes*

Amœba actually walks on its false feet (pseudopodia), although this fact was not discovered until after years of study by various

competent investigators. The discovery of how Amœba walks is a miniature historical romance. When these little animals were first discovered, the observers noted, just as you can note when looking at any Amœba under a microscope, that the ectoplasm bulges out at some point and the endoplasm flows out into the process. Thus the whole organism seems to flow forward in the direction of the advancing pseudopod. Sometimes two pseudopods start out in different directions and the Amœba seems to have a hard time to decide between two directions of advance. There is an apparent contest between the two pseudopods until one gives up and flows back, while the other flows more rapidly forward. It has long been a great problem to explain on mechanical grounds the formation of pseudopodia and the way in which they draw after them the rest of the body. The whole point of this problem lies in the fact that here we have a very simple case of spontaneous movement in protoplasm or of mechanical work done by protoplasm. If we could solve the mechanism of pseudopodial movement, we should have the key to other, more complex expressions of protoplasmic mechanics, such as ciliary activity or muscular contraction.

Four main theories have been advanced to account in physico-chemical terms for pseudopodial locomotion. A brief outline of each is presented herewith.

a. The Adhesion Theory.—According to this view, Amœba moves for the same reason that a drop of water or any other inorganic fluid placed on a piece of glass sometimes spreads irregularly instead of maintaining a circular outline. The explanation given is that the glass has an uneven surface, is not perfectly clean, but is slightly greasy in spots. Where the glass is clean, adhesion takes place more perfectly and the drop spreads out more rapidly, while it adheres less well to grease or other substances. Applying the adhesion theory to Amœba, it was supposed that the surface on which it moves is irregular as to its adhesive properties and that the pseudopods flow in the paths of greater adhesion. The weakness of this theory is that pseudopods are very frequently thrust out free, not in contact with any surface. Since contact of any sort is not a necessity the adhesion theory proves unsatisfactory.

b. The Surface Tension Theory.—Surface tension is a physical property of fluids which involves a tensile pull of the surface film.

It is believed to account for the spherical form of such objects as soap bubbles or drops of oil suspended in water; for the surface of these bodies has contracted to the greatest possible extent, in as much as a sphere has the least surface in proportion to its mass. According to ***Bütschli*** and ***Rhumbler,*** who proposed this theory, Amœba is a fluid body which would be spherical in a homogeneous medium, but in a heterogeneous medium like pond water it encounters conditions on one side that lessen the surface tension. At this weakened point the surface bulges out into a pseudopod. Constantly changing conditions cause the local weakening of surface tension to shift from one place to another and, consequently, the withdrawal of one pseudopod and the thrusting out of another. Experiments with rancid oil drops in aqueous solutions seemed to substantiate this theory; for they could be made to change shape and send out blunt processes when substances known to lower surface tension were applied locally to portions of the surface. It was noted that in a region of lowered surface tension currents were set up which flowed backward along the surface and forward in the center. ***Dellinger*** has demonstrated that currents in a pseudopod of Amœba do not flow in that way but in exactly the opposite directions; yet this theory held sway for some time in spite of its weaknesses.

c. Contraction Theories.—An early notion obtained that the thrusting out of pseudopods was due to protoplasmic contractility of some sort; but the ideas of the exact nature and location of the contraction impulse were somewhat naïve. Amœba was looked upon as a fluid-filled, elastic sac which could undergo contraction of parts of the surface, causing the weakest part of the wall to bulge out. According to this view, currents in the protoplasm should be observed first in the region of contraction and subsequently in the out-pushed region. But it was soon seen that currents begin at the point of pseudopod formation and not at the point supposed to be contracting—an observation which disproved the older contraction theories.

Two American investigators have reinstated the contraction theory by putting the matter in an entirely new light. ***Jennings*** had the ingenious notion of marking in some way the surface of an Amœba in order to watch the fate of any point under observation. This he did by dropping on an Amœba's back a particle of lamp black. This adheres firmly and furnishes a fine landmark by

means of which the relative rates of flow of ectoplasm and endoplasm can be followed and shifts in position of the ectoplasm may be mapped out. Jennings' diagram of a progressing Amœba is

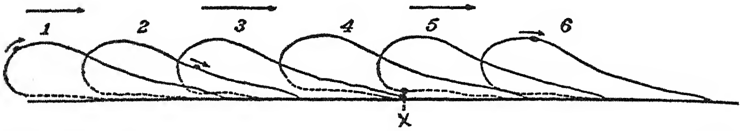


FIG. 89. Diagram of the movements of a particle attached to the outer surface of *Amœba verrucosa*, in side view. (From Jennings.)

shown in Figure 89. An analysis of the locomotion of an Amœba is thus given by Jennings:—

"In an advancing Amœba substance flows forward on the upper surface, rolls over at the anterior edge, coming in contact with the substratum, then remains quiet until the body of the Amœba has passed over it. It then moves upward at the posterior end and forward again on the upper surface, continuing in rotation as long as the Amœba continues to progress. The motion of the upper surface is congruent with that of the endoplasm, the two forming a single stream. The movement can be imitated roughly by making a cylinder of cloth, laying it flat on a plane surface, and pulling forward the anterior edge in a series of waves. The entire cylinder then rolls forward just as Amœba does."

Two points in connection with Jennings' work should be mentioned: first, that he does not state definitely the location of the contractile substances which pull the Amœba forward; second, he used a species of Amœba (*A. verrucosa*) which is almost devoid of pseudopodia and actually does seem to roll along as simply as he describes. The rolling theory, however, does not apply at all well to *Amœba proteus*.

We owe to ***Dellinger*** the best explanation of how Amœba walks. This author had frequently observed that small organisms swam under a large Amœba as though the latter were supported on legs. This gave him a clue to the real situation. If one were to try to discover the mode of locomotion of a horse by looking down upon it from the top of a skyscraper, he might get an entirely wrong impression: so with Amœba. We have always looked down upon Amœba from a great height above. Dellinger conceived the idea of looking at the animal from the side exactly as one would look at a horse from the sidewalk. He made a promenade for the

Amœba in the following way: one edge of a glass slide was ground smooth and flat. Two long cover slips were cemented with edges protruding somewhat beyond the flat edge of the slide, as shown in Figure 90. The microscope was then bent over into a horizontal position, thus bringing the troughlike slot of the slide uppermost and putting the flat surface parallel with the earth's surface. Amœbæ were then placed in the trough along with water, and observations and microphotographs were taken as they paraded before the observer. Dellinger noted that advancing Amœba "extend the anterior end free in the water and attach it at or near

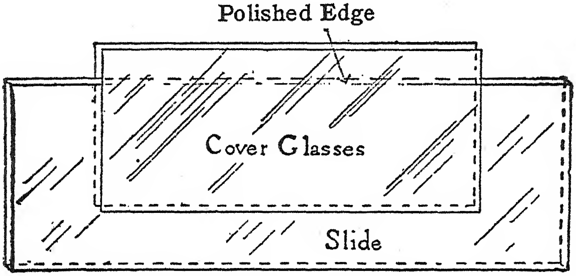


FIG. 90. Diagram of apparatus used for the study of locomotion in Amœba. By mounting this slide in a horizontal microscope the Amœbæ may be seen in side view. (From Dellinger.)

the tip and then contract. At the same time the posterior end is contracting and the substance thus pushed and pulled forward goes to form the new anterior end. This continues as long as the Amœba advances [Fig. 86, **D**, **E**, **F**]. Often the anterior end is pushed along the substratum but no attachments form except at definite points. . . . In other cases the anterior end is lifted free and then curves down to the substratum and attaches, forming a long loop. The posterior end is then released, and the substance flows over to the anterior end. At the same time another anterior end is extended." Dellinger showed that Amœba can walk on the ceiling as well as the floor. The important point to note is that the animal actually *walks*, putting one foot out and then another. When a forward step is made, a foot (pseudopod) is stretched out, takes hold and then shortens (contracts). This is the locomotor act: for contraction involves mechanical work. We do not know for certain exactly what makes a pseudopod extend and then contract, but the prevailing theory is that proto-

plasm, especially the ectoplasm, is a colloid substance that goes into the sol state when it takes up water and tends to flow outward. Attachment is believed to stimulate the reverse phase of the protoplasm, causing it to lose water and assume the gel state and thus to contract locally. There is a rhythmic alternation of exchanges of water between the ectoplasm and endoplasm, and this causes alternate contractions and expansions. If this be the correct explanation of pseudopodial movement, it is not unlikely that all rhythmic protoplasmic movements, such as those in cilia or those in muscle fibers, are due to the same reversible changes in colloids.

d. Mast's Theory.—The latest interpretation of the mechanics of locomotion in Amœba has been worked out by ***S. O. Mast*** and his pupils. Working with relatively simple Amœbæ, they have been able to determine that the forward flow of the pseudopod is caused by contraction of the more viscous ectoplasm, especially in regions back of the pseudopodia. There is a forward current in the more fluid endoplasm which causes an outflow at points where the ectoplasm is thinnest and least solid. As the plasmasol flows out through the aperture it becomes transformed into plasmagel around the base of the pseudopod, building it out "much as a chimney might be extended by carrying bricks and mortar up through it and depositing them on the wall surrounding the opening." To carry out this figure, it must be supposed that the wall at the bottom of the "chimney" is constantly undergoing disintegration into bricks and mortar, thus providing more material for transportation to the top. Thus plasmasol changes to plasmagel at one end and the reverse change takes place at the other. The flow is initiated by contraction of the ectoplasm and a sort of bursting forth of the endoplasm to form pseudopods. This latest view then appears to be a refinement of the earlier contraction theories. The student will readily gather that even such a relatively simple problem as that of the mechanism of locomotion in Amœba is as yet incompletely solved.

3. *The Behavior of Amœba*

All activities of the whole organism in response to internal or external stimuli are included within the definition of the word "behavior." Many studies have been made of the ways in which Amœba responds to different kinds of external stimuli. ***Jennings***

has grouped the reactions of Amœba into positive responses, negative responses, and food-taking responses. We have already dealt with the food-taking reaction, and shall omit further consideration of this process.

When a stimulus strikes an Amœba, it behaves as though it either likes it or dislikes it. If it likes it, it moves toward it or at least it goes on undisturbed. If it dislikes it, it moves away. The words "like" and "dislike" are open to objection. Instead, let us say that an Amœba that reacts favorably toward light, for example, is positively phototactic or exhibits positive phototaxis; that, if it reacts unfavorably to light, it is negatively phototactic. The movements toward or away from the stimulus are called TROPISMS. Thus we speak of positive and negative phototropism.

In Amœba we distinguish the following tropisms:—

1. Phototropism (reaction to light),
2. Thermotropism (reaction to heat),
3. Thigmotropism (reaction to contact),
4. Chemotropism (reaction to chemicals),
5. Galvanotropism (reaction to the galvanic current),
6. Geotropism (reaction to gravity),
7. Rheotropism (reaction to currents).

Amœba reacts to all of these stimuli in either a positive or a negative way. Sometimes a positive response will be given to a stimulus of a certain intensity, and a negative response to one of a greater or less intensity. Studies of the behavior of Amœba under a great variety of stimuli have shown that it behaves in much the same ways as do higher organisms. This has interested the students of psychology. They feel that a complete understanding of Amœba's activities might reveal the beginnings of mind, of intelligence. Without going into detail in this place, it may be said that Amœba seems to show evidences of possessing mental faculties which are, in the words of Jennings, "comparable to the habits, reflexes, and automatic activities of higher organisms" and, "if Amœba were a large animal, so as to come within the everyday experience of human beings, its behavior would at once call forth the attribution to it of states of pleasure and pain, of hunger, desire, and the like, on precisely the same basis as we attribute these things to a dog." It is no more difficult to believe that Amœba has a kind of mind than that a germ cell has a mind. Yet, according to ***Conklin*** an egg cell or a spermatozoön has sensi-

tivity and responds to stimuli by appropriate tropisms or reflexes, thus exhibiting the beginnings of mental activity. A germ cell and an Amœba probably possess minds of about the same sort.

D. Reproduction in Amœba

The life cycle of *Amœba proteus* is unexpectedly complex for so lowly an organism. According to ***Calkins*** who has studied the life cycle in great detail, Amœba has an infancy, a youth, a period

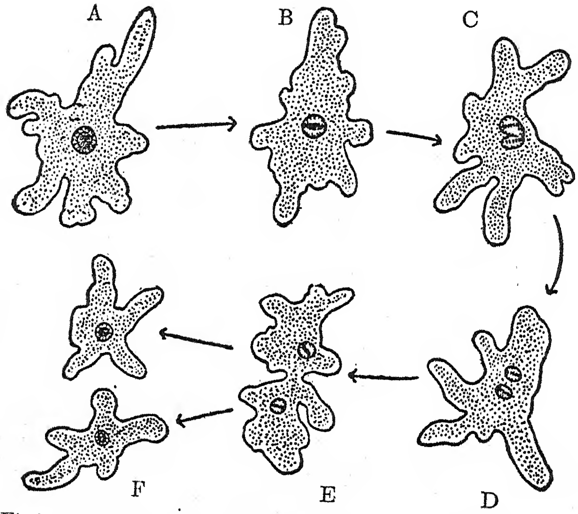


Fig. 91. Fission of *Amœba*. A, *Amœba* before the onset of fission; B, most of the chromatin has become concentrated in chromosomes about the equator of the nucleus; C, each chromosome has divided into two, the two sets of daughter chromosomes are moving apart and the boundary of the nucleus is becoming indented between them; D, the nucleus has become completely divided into two daughter nuclei; E, the two nuclei have moved apart and the cytoplasmic body of the *Amœba* is undergoing constriction; F, the process has been completed. (From Hegner, after Kerr.)

of maturity, and an old age. Starting out as a tiny thing called a pseudopodiospore, which has but one pseudopod, it goes through a period of growth and increasing complexity until it reaches the full-grown stage. When it reaches the maximum size, it divides by binary fission (Fig. 91) into two daughter Amœbæ. Each of these grows to twice its initial size and binary fission again occurs. How many times this phase of multiplication may be repeated

depends upon the particular strain of Amœba used and the favorableness of the environmental conditions. During binary fission the nucleus sometimes appears to divide by amitosis, but more often clear evidences of a sort of simplified mitosis are observed (Fig. 92). After the period of binary fission comes to an end a period of encystment and sporulation intervenes. This appears to be a very complicated process and the observers of the process fail to agree upon its details. Obviously, however, the period is one of senescence. The final stage is the formation of pseudopodiospores—essentially infant Amœbæ. Thus we are back where we started. This cyclical feature of reproduction is universal for organisms and is dealt with here to emphasize that Amœba in one stage may be fairly simple, but when we come to study all of its varied phases, it loses for us its simplicity and makes an impression of confusing complexity.

FIG. 92. *Amœba binucleata* beginning to divide. Both nuclei have formed mitotic figures. (From Lang, after Schaudinn.)

SUMMARY

1. *Amœba proteus*, the species most studied in the laboratory, belongs to the Subkingdom Protozoa and the Phylum Rhizopoda, which is characterized by the presence of pseudopodia. There are many species of the genus Amœba.

2. Amœba is characterized by changing form and shifting axis, by the fact that the nucleus and contractile vacuole move about within the endoplasm, by its primitive method of engulfing food, by its lack of any shell or protective layer on the surface, and by its lack of a definite sexual phase in its reproductive cycle.

3. Though the protoplasm of Amœba is only slightly specialized as compared with other Protozoa, it is capable of carrying on much the same functions as are carried on in higher organisms, including digestion, assimilation, respiration, response to stimulation, growth, and reproduction.

4. A great deal of study of amœboid locomotion has been undertaken in the belief that, if an understanding of the exact mechanism of this process were attained, light would be thrown upon the whole problem of mechanical action in protoplasm. The various theories of the mechanics of pseudopodial movement are presented and criticized.

5. Amœba exhibits a type of behavior, or response of the whole body

to environmental stimuli, that is called tropistic. The tropisms of Amœba are considered as "comparable to the habits, reflexes and automatic activities of higher organisms."

6. Amœba reproduces by binary fission, involving a special type of mitosis. At intervals, binary fission is interrupted by a more complex mode of reproduction, the details of which are still obscure.

CHAPTER XVI

PARAMECIUM
(SUBKINGDOM PROTOZOA)

Paramecium caudatum and *P. aurelia* are zoölogical classics. While the first species is somewhat commoner, the latter is more frequently figured in the illustrations. Paramecium is called the "slipper animalcule" because of a fancied resemblance to a crude slipper. In outline one can see that the anterior end is blunt and narrow like the heel and that the posterior end is broader and pointed like the toe. Perhaps the oral groove may be thought of as like the opening to the inside of the slipper. Paramecium is one of the most abundant of Protozoa and is perhaps the most readily obtained for laboratory work. It is therefore a favorite denizen of the zoölogical laboratories. Quite commonly one finds Amœba and Paramecium living together in the same environment. While Amœba may be considered as a good example of the simpler types of Protozoa, Paramecium may be contrasted with it as one of the more complex members of that group.

A. General Morphology

1. *Paramecium and Amœba Contrasted*

Amœba was seen to be a shifty individual, never looking the same any two successive minutes, with a changing axis and with a nucleus and contractile vacuoles floating about in the endoplasm. Paramecium (Fig. 93), on the other hand, has a fixed axis, with permanent anterior and posterior ends and a permanent semi-spiral groove—the ORAL GROOVE—running from the anterior end down to the permanent MOUTH. The mouth opens into a funnel-like depression called the CYTOPHARYNX, or GULLET. Instead of temporary locomotor organs like the pseudopodia of Amœba, Paramecium has the entire surface covered with numerous whip-like motor organs called CILIA. The ectoplasm is covered with a thin, tough CUTICLE, or PELLICLE. Under this there is a definitely differentiated layer called the CORTEX, which contains closely

packed TRICHOCYSTS that give this layer somewhat the appearance of a cellular layer. The endoplasm is fluid, as in Amœba, but both the MACRONUCLEUS and MICRONUCLEUS, as well as the two CON-

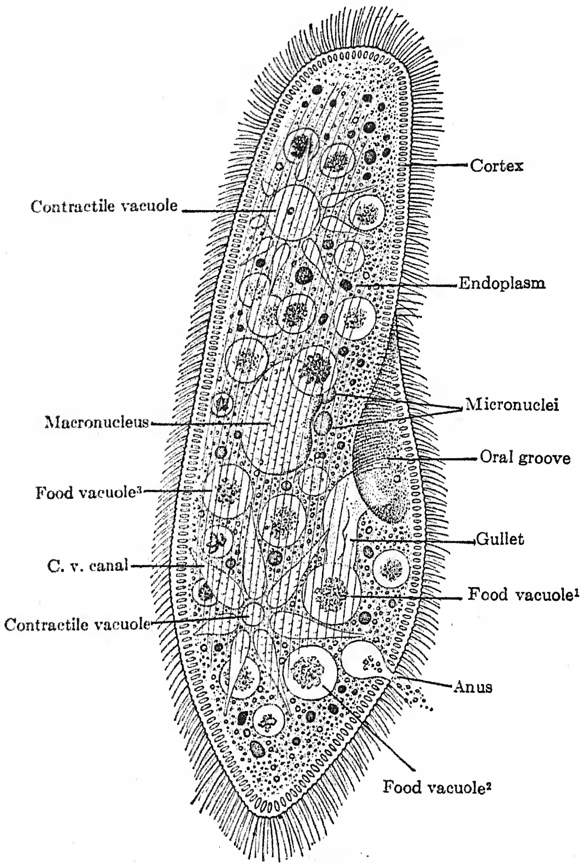


FIG. 93. *Paramecium aurelia.* Note especially the two micronuclei. (Redrawn after Pfurtscheller wall chart.)

TRACTILE VACUOLES appear to be anchored definitely at fixed points. There is also a fixed ANUS situated just back of the oral groove.

The general impression one gets from a comparison between Amœba and Paramecium is that the latter has a much more highly specialized organization: its organs are much more definite and

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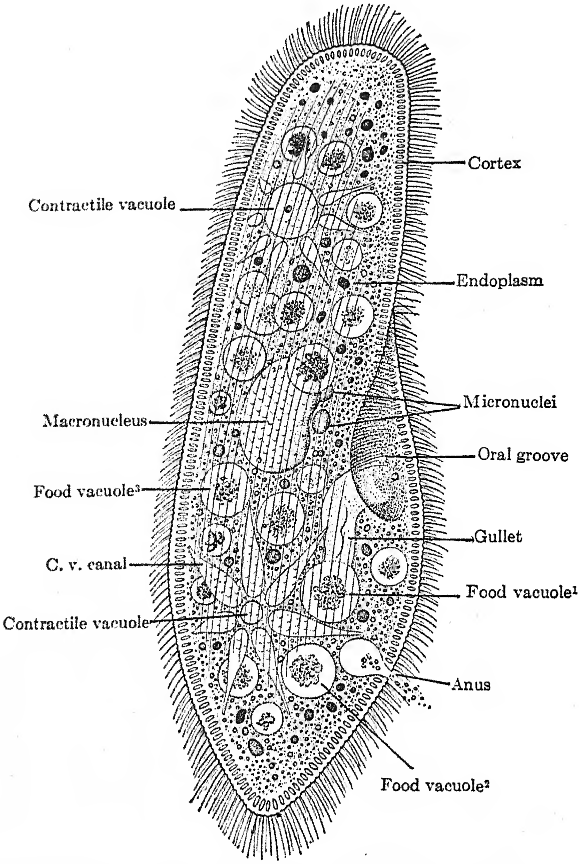

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The general impression one gets from a comparison between Amœba and Paramecium is that the latter has a much more highly specialized organization: its organs are much more definite and

fixed. If one were asked to say which is the higher organism, one would undoubtedly answer that Paramecium is higher. When pinned down as to what is meant by higher or lower, one would have to reply that it is all a matter of degree of specialization. Paramecium is probably no more capable of meeting the world struggle than is Amœba. Both must be eminently successful and well-adapted animals, else they could hardly have survived all these ages of competitive life. One is as fit as the other. Perhaps we are all wrong in ranking one organism as high and another low. This at least is a problem that the student had best be thinking about as he surveys various animal groups.

2. *Finer Details of Structure*

The permanency of form of Paramecium is due to the fact that the ectoplasm is a well-defined, fairly stiff body wall. The external layer, or PELLICLE, is a separate layer which can be blistered free from the cortex by adding a little weak alcohol to a drop of water containing Paramecia. The pellicle, viewed from the surface, appears to be sculptured into rows of hexagonal areas, each of which has a cilium attached to its center (Fig. 94, A). Between the hexagonal areas occur little pores that seem to be holes through which TRICHOCYSTS are extruded. Trichocysts are characteristic structures of the cortex (the layer of ectoplasm beneath the pellicle). These bodies are arranged perpendicularly to the surface (Fig. 94, B). Just what trichocysts are, how they arise, and how they function, are matters incompletely understood. They seem to be semi-fluid in consistency; they arise in the endoplasm near the nucleus, possibly being a product of the latter; they migrate to the exterior and locate themselves in a very accurately spaced fashion. When the animal is strongly irritated, the trichocysts are discharged as long sticky threads through pores in the pellicle. The trichocysts serve primarily as organs of defense in that they adhere to and entangle organisms, such as Didinium, that attack Paramecium (Fig. 95).

The ENDOPLASM has a bubbly or alveolar appearance. There are in it many food vacuoles and various large granular bodies which are probably reserve food materials. The whole endoplasm seems to circulate about in one distinct current which carries with it the food vacuoles and all other movable structures. Such a food path may be likened to an alimentary tract.

The two CONTRACTILE VACUOLES can hardly be assigned definitely to either ectoplasm or endoplasm. They seem to be mainly in the latter but are definitely fastened to the former. Their posi-

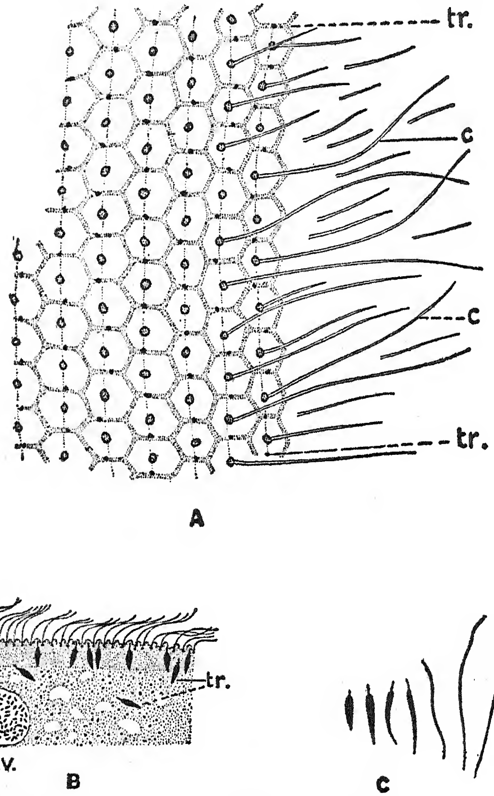


FIG. 94. Structural details of *Paramecium.* A, surface view of the pellicle, showing hexagonal areas produced by striations; tr., the position of the ends of the trichocysts; and the cilia, c. B, part of a cross section of the surface of *Paramecium* showing surface ridges, cilia attached to microsomes and trichocysts, in black, cut longitudinally and usually lying in the ectoplasm, though some are seen arising in the endoplasm; f.v., a food vacuole in the endoplasm. C, seven stages in the discharge of trichocysts; the one of the left just beginning to discharge and that on the right completely discharged. (Redrawn, A, after Schuberg; B, C, after Maier.)

tion is on the ABORAL surface (that away from the mouth). Each vacuole is provided with from six to ten long radiating canals that reach out so far as to communicate with most of the parts of the body. Each canal receives water from the endoplasm that lies in

contact with it. When the canals are all full and distended at their inner ends, they simultaneously discharge their contents into the vacuole, which then contracts and forces the liquid out through a pore in the pellicle. Then the canals fill again. The two contractile vacuoles work alternately, one being in the full condition while the other is empty. The rhythm of discharge of the vacuoles in a quietly feeding individual is rather exact, for one can note that a definite time interval elapses between discharges. The functions of the contractile vacuoles are doubtless the same as those described for Amœba. It has recently been shown by Weatherly that the function of the vacuole (in Paramecium) is not the elimination of nitrogenous waste products of metabolism, but is probably the regulation of hydrostatic pressure within the cell. The method of feeding necessitates taking a great deal of excess water, and if this could not be eliminated fast enough the animal would swell up and dissolve in the excess of water.

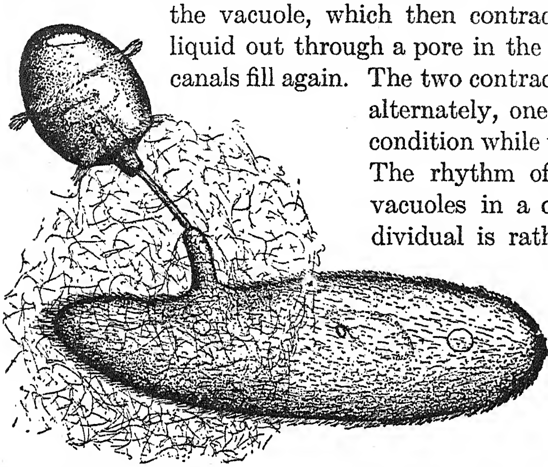


FIG. 95. *Paramecium* making use of its trichocysts in defending itself against the attack of *Didinium*, a predaceous protozoan. The mass of trichocysts swells up into a voluminous jelly and seems mechanically to force the enemy away. (From Mast.)

B. Physiology of Paramecium

1. *How Paramecium Swims*

The Equipment of Cilia.—The swimming unit is the CILIUM (plural, CILIA), a whiplike process projecting from the center of each hexagonal area of the pellicle. The cilia at the posterior end in *Paramecium caudatum* are longer than elsewhere and this little caudal tuft has given it the specific name, *caudatum* (meaning tailed). A cilium is believed to be equivalent to a long, permanent pseudopod. The mechanics of ciliary motion is still an unsolved problem, but in the light of what we have discovered about the

basis of pseudopodial movement, it seems highly probable that the movement is due to rhythmic contraction and expansion of colloidal elements in the cilium. Flagella, which are much like cilia in structure and in function, have been shown to have distinct contractile fibrils running throughout their length, and it is probable that cilia are similarly constructed. This theory would imply that, when the animal is moving forward, fibrils on the posterior side of each cilium contract more strongly than those on the anterior side. When the animal moves backward, however, as it frequently does when avoiding unfavorable regions of the environment, the anterior contractile substances contract more vigorously than the posterior. The cilia of the oral groove and of the mouth are stronger and more vigorous than elsewhere, and serve to cause a vortex of water to be pulled into the mouth. This serves as a feeding mechanism. The cilia of the dorsal part of the oral funnel, or mouth, are fused together side by side into a flat sheet called the UNDULATING MEMBRANE, which serves the function of guiding food particles into the mouth.

Neuromotor Mechanism.—The secret of the finely coördinated activities of the elaborate system of cilia in Paramecium has been revealed by ***Rees***. By special staining methods he has shown that, radiating from a coördinating center near the gullet, which is called the MOTORIUM, are numerous very delicate protoplasmic fibrils which run to all parts of the surface and seem to connect with the individual cilia (Fig. 96). In this way, an adverse stimulus from materials entering the gullet may be transmitted at once to all cilia so that they reverse together and cause the animal to swim backward. This motorium with its neurofibrillæ may be regarded as a sort of central nervous system within the bounds of a unicellular body. The addition of this system to an already complex organization increases our conviction that Paramecium, though unicellular, is really very complex.

The Spiral Path of Paramecium.—When Paramecium swims through the water, it does not follow a straight course but, when unobstructed, describes a distinct spiral, such as one would describe in going up a steep spiral staircase. The explanation of this spiral course is somewhat complicated. In the first place, the beat of the cilia is not straight backward but diagonally over to the left. This would, of itself, make the animal go forward in a straight course, spinning on its long axis like a shell shot from

the rifled bore of a cannon. In the second place, the beat of the cilia in the oral groove is much stronger than elsewhere and is continually pulling a vortex of water toward the oral surface. This has the same effect as pulling the oral groove side of the Paramecium off its course. As the animal is continually revolving, the oral groove is pointed successively to all radii of the axis, and that produces the spiral course. This may need a little figuring out on the part of the student. If a Paramecium could be attached by its tail to a swivel and its ciliary action kept up as in normal locomotion, it would describe a cone. Imagine this cone projected forward and you would have a spiral. The adaptive features of the spiral path, as discussed by Jennings, are that the spiral path, as contrasted with a straight course, affords a much more extensive range for food hunting operations. As Paramecium goes forward it dives now up, now down, now to one side, and now to the other, and always it draws in a cone of water from ahead of it. If the cone of water contains food, the direction is altered so that the animal runs into the food region. If, however, the animal went straight ahead like a

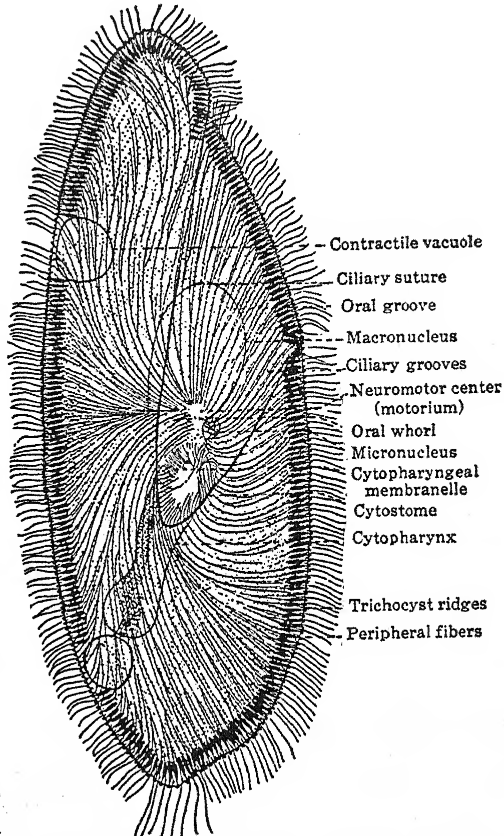


FIG. 96. *Paramecium caudatum.* Neuromotor mechanism, showing the neuromotor center (motorium) and neurofibrillæ connecting with cilia and trichocysts. (From Hegner, after Rees.)

bullet, it could not cover anything like so much territory and its chances of finding food would be correspondingly less. It will soon be shown how the spiral path aids in keeping out of danger.

2. *How Paramecium Feeds*

We have already shown how Paramecium hunts for food. When it enters a region of abundant food, such as a mass of bacteria, it seems to quiet down and come to rest. The stimulus of the food seems to act as a depressant upon the body cilia and they move very slowly; but the cilia of the oral groove show increased activity. A vortex of food-laden water is swept down the oral groove and is focused by means of the undulatory membrane into the mouth. So forcibly does the vortex of water play upon the naked protoplasm inside of the mouth that a pocket is made in the endoplasm (see Fig. 93). The pocket grows larger and larger like a bubble on a bubble pipe, and bacteria continue to collect within it until the bubble breaks off and floats away with its load of food. It is then a FOOD VACUOLE. Vacuole after vacuole is formed in this way, and they move off as though caught in a current and follow one another in a procession. As the food vacuoles drift along a well-defined path, which is functionally equivalent to a digestive tract, the process of digestion takes place; the digested food is passed out into the surrounding protoplasm, assimilated, and used up in energy and growth. It has already been shown how the contractile vacuoles serve to remove the excess water from the food vacuoles. All that now remains is for the indigestible material to be discarded. This takes place when the old food vacuoles drift to the posterior end and give off their débris through the ANAL OPENING.

3. *Behavior of Paramecium*

Paramecium has been used as experimental material by many investigators interested in the analysis of the behavior of lower organisms. It has been discovered, as was the case for Amœba, that Paramecium exhibits in more or less definite fashion all of the types of tropism. There is practically no controversy as to the *fact* that the animals are guided by stimuli of all sorts so that they collect in regions of favorable stimuli and depart from regions of unfavorable stimuli. The real controversy centers about the exact *method* by means of which Paramecium directs its course to or from

the sources of stimulation. Two contrasting interpretations of the directed behavior of Paramecium, and similarly of many other animals, have been offered: the one implying that the organism is a pure automaton driven helplessly by the external forces, and the other that the organism has a good deal to do with directing its own course and choosing its own location. The former is the Tropism Theory of animal behavior and the second the Trial and Error Theory.

Tropism versus Trial and Error.—A decade or so ago zoölogists were much more interested in the analysis of the behavior of the lower organisms than they are today. Most of the pioneer work in the field of animal behavior was done by the zoölogists; but now this field has been lifted almost bodily out of the zoölogical laboratories and transferred to those of comparative psychology. Some zoölogists with ecological propensities are still interested in animal behavior as a phase of the response of organism to environment. While interest in animal behavior was still strong and fresh among zoölogists, two distinct schools of animal behaviorists developed. One school, strongly inclined to take an extreme mechanistic attitude toward animal responses, looked upon Paramecium, for example, as a helpless, blind automaton driven about by external stimuli after the fashion of John Hayes Hammond's automatic torpedo. This torpedo is provided with selenium cells on the two sides, which are so sensitive to light that a searchlight thrown on the moving torpedo from straight behind stimulates both sides equally; but if it turns to one side, the selenium cell of the side nearer the light is more affected and operates some mechanism that will straighten the course. Paramecium is thought to be thus guided by stimuli in such a way that when the directed lines of energy strike it on one side, they will either stimulate or quiet that side, thus rendering the beat of cilia on the two sides unequal in strength. This will cause the animal to turn until the two sides are equally stimulated, when it will swim directly toward or directly away from the stimulus. This is, in outline at least, a statement of the tropism theory of animal behavior as applied to Paramecium by the late ***Jacques Loeb.***

Professor H. S. Jennings was the first to take issue with this theory. In his studies of Paramecium under all sorts of environmental conditions he was never able to see any evidence that Paramecium behaved in this simple, direct fashion. Anyone who

observes the animals swimming about gets quite a different impression of their activities. They seem to start, stop, back up, start off in another direction, and never to maintain a straight course. Jennings' explanation of why a Paramecium comes to find the most favorable part of its environment is quite different from that implied in the Tropism Theory. When a Paramecium is swimming forward in a spiral path, testing the water ahead and to one side of it by means of the test cone of water drawn into the oral groove, it comes to a region where the content of the water is unfavorable. If markedly unfavorable, the animal gives a prompt negative response, the so-called "AVOIDING REACTION" (Fig. 97). The direction of ciliary beat is suddenly reversed, sending the animal

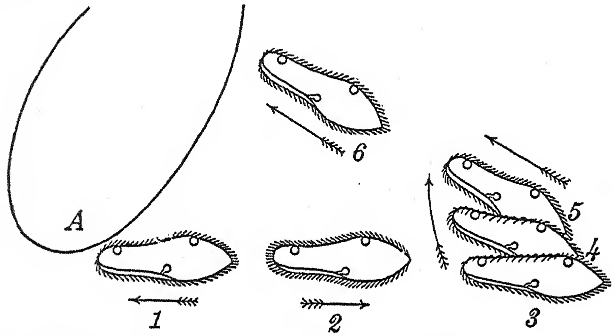


FIG. 97. Diagram of the avoiding reaction of *Paramecium*. *A* is a solid object or other source of stimulation. *1–6*, successive positions occupied by the animal. (The rotation on the long axis is not shown.) (From Jennings.)

backward for a short distance until it is out of range of the adverse stimulus. Then the forward beat of cilia is resumed. While overcoming the momentum of the backward motion, the body simply whirls on its tail like a top slightly off balance, the anterior end describing a circle. As it spins around, the oral groove samples the water in all directions, and, when the sample is satisfactory, forward progress is resumed along one of the axes of the cone which the body is describing. This spinning around and trying a number of directions before selecting a favorable one is called the TRIAL AND ERROR method of orientation. The avoiding reaction and the trial and error process may be repeated a great many times and doubtless will be kept up as long as there are unfavorable stimuli in the environment. When Paramecium by this more or less experimental method finally gets into the most favorable neighbor-

hood, it either comes to rest for feeding purposes or, if still stimulated, keeps moving about. Whenever it swims toward a less favorable region, the avoiding reaction drives it back, and it is thus practically trapped in the favorable region, unable to get out of it. That is Jennings' explanation of why we find great aggregations of Paramecia on one side or other of a dish placed in some position where light enters from one direction. By continually avoiding the less favorably lighted regions they finally come to comparative rest at the region of optimum (most favorable) light intensity. Thus they are not forced directly into the favorable region or away from the unfavorable region, as the Tropism Theory claims, but reach their destination in a much less direct fashion, by trying and trying, rejecting and rejecting, until finally, more or less by chance, the best region is found. When once the most favorable region is found, the animal will give the avoiding reaction to all regions less favorable. This whole explanation of Professor Jennings seems to imply that Paramecium is not a pure automaton driven by forces outside of itself, but that it is very much in control of its own activities. Some critics have claimed that this view borders on a vitalistic interpretation, but this criticism is quite unjustified. Though small in size, Paramecium is not a very simple organism and it behaves very much like many metazoan organisms. It is only when we ignore the organic complexity of the Protozoa that we make the mistake of oversimplifying their activities. The activities of Paramecium compare very favorably with those of Metazoa as high in the scale as worms and mollusks. Moreover, even human beings learn by trial and error: we try a variety of methods of doing a thing and select the most effective one; we have our avoiding reactions, our protective reflexes of various sorts; and many of our mental activities are as automatic as those of Paramecium.

C. Reproduction and the Life Cycle of Paramecium

The life cycle of Paramecium is a complex one, involving many intricate changes in both nucleus and cytosome. It consists of a series of divisions of whole individuals by transverse binary fission, interrupted at long intervals by a temporary union or conjugation of two individuals—the latter a sexual act. There is thus a sort of alternation between asexual and sexual reproduction.

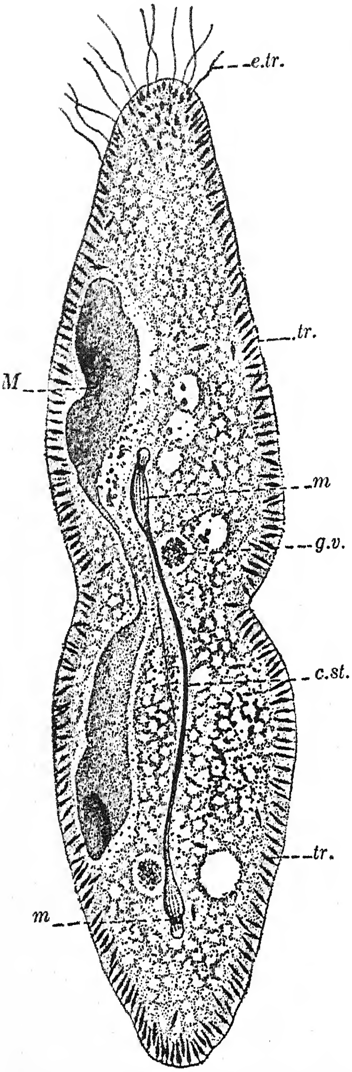


FIG. 98. Section of a dividing *Paramecium caudatum*. *M*, dividing macronucleus; *m*, *c.st.*, dividing micronucleus; *g.v.*, gastric vacuole; *tr.*, trichocysts; *e.tr.*, extruded trichocysts. (From Woodruff, after Calkins.)

Binary Fission.—When a Paramecium is about to begin fission the micronucleus—there are two of these in *P. aurelia*—the small inconspicuous body that normally lies imbedded in the side of the much larger macronucleus, leaves its position and undergoes a peculiar sort of mitotic division (Fig. 98). In the anaphases the mitotic figure is long and slender with knoblike ends where the daughter chromatin lies; while in the middle the spindle of fibers is much like that seen in typical mitotic division. Subsequently the middle parts of the spindle fade away, leaving the two rounded ends widely separated, one near the anterior and one near the posterior end of the individual. The macronucleus follows suit, elongates, and becomes dumbbell-shaped; the two halves pull apart and nuclear division is complete. The gullet buds off a small posterior branch which migrates backward to form the gullet of the posterior daughter individual. The undulating membrane remains in the old gullet and a new one arises in the new gullet. A new contractile vacuole arises in each of the two prospective individuals. While these changes have been in progress a constriction has arisen around the body at about equal distances from the two ends. This cuts deeper and deeper into the body

until the last threadlike junction between the two bodies is broken and two completely separate daughter individuals are produced. This all takes place in about two hours, more or less, depending on the temperature and other growth controlling factors. Normally, this process is repeated about once every twenty-four hours, and it may continue without variation for weeks or even months. The daughter Paramecia are not exactly like the parent at first, and they also differ from each other, for they have been derived from two quite different portions of the body. Moreover, each is only half as large as the parent. A period of DEDIFFERENTIATION ensues, during which the structural differences between the two are gradually done away with, and each individual then redifferentiates the structural characteristics of its species and grows up to full size.

Heredity.—It is easy to understand why a daughter Paramecium inherits its characters from its parent. It is merely a continuation of the parent, for the production of offspring eliminates the parent. The PHYSICAL BASIS OF HEREDITY is well illustrated here. An offspring resembles the parent because it arises through the isolation from the parent body of a representative living part of the latter, a part endowed with a capacity to redevelop the specific differentiations possessed by the parent.

Conjugation.—There are some nonconjugating strains of Paramecium, but the rule is that after a certain number of fissions, varying in different strains, conjugation ensues. An experienced investigator, watching his pedigreed cultures from day to day, soon learns to detect the signs of approaching conjugation. The individuals look unhealthy, appear somewhat opaque, and move about as though excited. When two Paramecia are ready to conjugate, they come into contact by their oral surfaces and adhere in this position because of the sticky character of the surface protoplasm. At about the middle of the surface of contact a protoplasmic bridge is formed, uniting the internal protoplasms of the two individuals. This union, together with the ensuing events, is interpreted as a sexual act.

Our attention must now be focused upon the changes in the micronucleus, which up till now has been quiescent, imbedded in the side of the macronucleus. The micronucleus (two of these in *P. aurelia*) frees itself and then undergoes a mitotic division about like that described for binary fission. Almost immediately the

two daughter nuclei divide again, making four. Three of these resultant micronuclei disintegrate, while the fourth divides again into a smaller and a larger nucleus. In each animal the smaller nucleus migrates across the protoplasmic bridge, enters the other individual, and fuses with the larger nucleus of that individual. Both individuals have thus exchanged nuclear material and now possess a new nucleus composed of chromatin materials from two individuals. This whole series of changes has been compared to the processes of maturation and fertilization of germ cells in the Metazoa, and doubtless there is a deep-seated analogy between the two processes. The two preliminary divisions remind one of the two MATURATION DIVISIONS in Metazoa, which result in the formation of four cells out of one, and especially call to mind the maturation divisions of the egg in which are produced one functional egg and three abortive eggs, or polar bodies. There is no division in Metazoa corresponding to that which gives rise to the stationary and the migrating nucleus; but the large stationary nucleus is like an egg nucleus, while the small migrating nucleus is like the sperm nucleus. Finally, the union of the two nuclei appears to be the equivalent of FERTILIZATION. The story of conjugation in *P. aurelia* is shown diagrammatically in Figure 99.

Soon after fertilization the CONJUGANTS separate. Even before separation, however, the macronucleus has begun to show clear signs of a break-up. It becomes irregular in shape, constricts, breaks into pieces, and these disintegrate more or less completely, leaving only a few dispersed granules. While the macronucleus has been disintegrating, the fusion nucleus has divided three times, giving rise first to two, then to four, and finally to eight micronuclei, four located near one end and four near the other end. The fate of these eight nuclei has been studied by various authorities and their accounts differ in minor details. One account has it that the four micronuclei near the anterior end enlarge and transform themselves into four macronuclei. Of the posterior group of four micronuclei, three disintegrate and dissolve up into the cytoplasm, the remaining one becoming a new micronucleus. This then divides and the process of fission is resumed. Probably the only difference between these earliest fissions and subsequent ones is that the four macronuclei have been preformed and need only be distributed to four prospective individuals. These two distributing divisions occur at short intervals. From

then on, the binary fission period is kept up until it is time for another conjugation.

The first few fissions are rapid and have been compared to the period of youth; the later divisions that go on for some time are

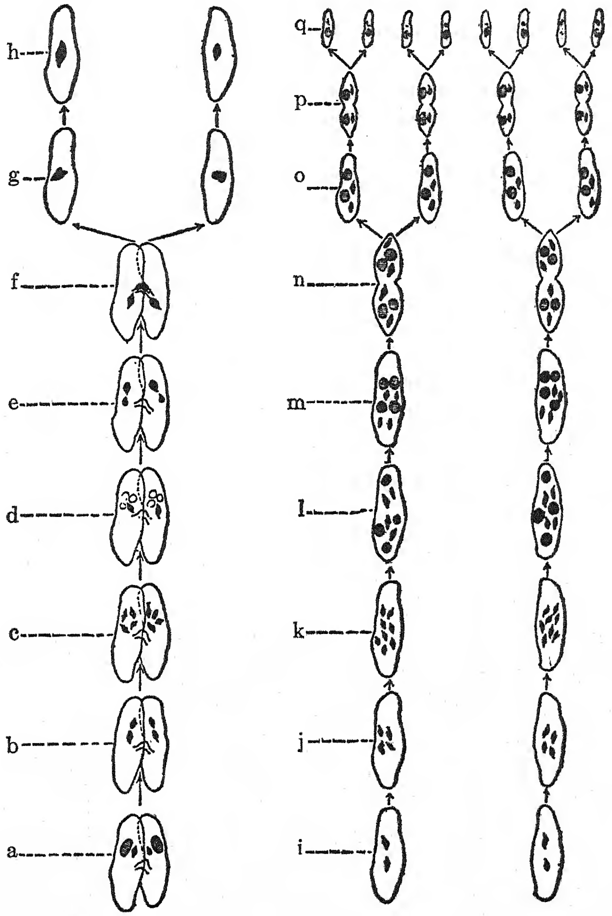


Fig. 99. *Paramecia* conjugating. a–q, stages in the nuclei during conjugation and the subsequent divisions of the conjugants during the period of nuclear reconstruction. The original macronuclei have been omitted except in stage a. (From Hegner, after Calkins and Cull.)

comparable to the period of maturity; and the period just before conjugation corresponds to the period of old age. If a Paramecium of a conjugating race cannot conjugate, it dies. Conjugation ap-

pears to be to some extent a process of reorganization or rejuvenation.

The Problem of Age and Natural Death.—It has been said that, except as the result of accident, Paramecium never dies. The body of one individual goes on living in the daughter individuals derived by fission. The parent ceases to exist but it does not die. After a long series of fissions the individuals grow old and would die, often do die in fact; but life may be saved by conjugation which involves a complete reorganization of all parts of the body, a breakdown of old structures and a rebuilding of new. The protoplasm takes a fresh start, becomes, as ***Calkins*** so aptly says, "germinal." Conjugation is believed by him to transform ordinary body cells into germ cells. An individual after conjugation is like a fertilized egg, or an organism in its earliest infancy: vigorous, renewed in its energy. We shall see later on that the physical immortality of Paramecium is no different from the physical immortality of germ cells of the higher organisms. The parent lives on in its offspring although part of it dies, namely, that part which has become specialized for maintaining the life of the individual. Even tissue cells of the higher organisms can go on living indefinitely if placed in proper culture media. Nerve cells, connective tissue cells, muscle cells, have been caused to grow when removed from the body. Natural death then is not due to any necessary playing out of vitality in individual cells, but seems to be "due to some defect in the interrelations of the many differentiated cells and organs of the body of the Metazoa and a defect which is cumulative until the organisms are unable to carry on the necessary functions, and die."

Is Conjugation Necessary?—If conjugation serves as a means of rejuvenating a race of Paramecia that has run down or become senescent, could other agencies accomplish the same end? ***Woodruff***, working with a race of Paramecia that was conjugating every six months, showed that by making a daily change in the culture medium he was able to prolong the unbroken series of binary fissions for a good many years. It appears then that the same rejuvenating effect is attained by a varied food as is normally attained by conjugation.

The same author discovered one race of *Paramecium aurelia* that never conjugates. For seven years this race was watched with care and there were no signs of conjugation nor of lowered

vitality. On microscopic examination, however, it was found that at regular intervals the separate individuals went through the same nuclear behavior as if they were conjugating, except that no nuclear material was exchanged between different individuals. This so-called ENDOMIXIS (Fig. 100) is interpreted as the equiva-

A

B

C

D

E

F

G

H

I

J

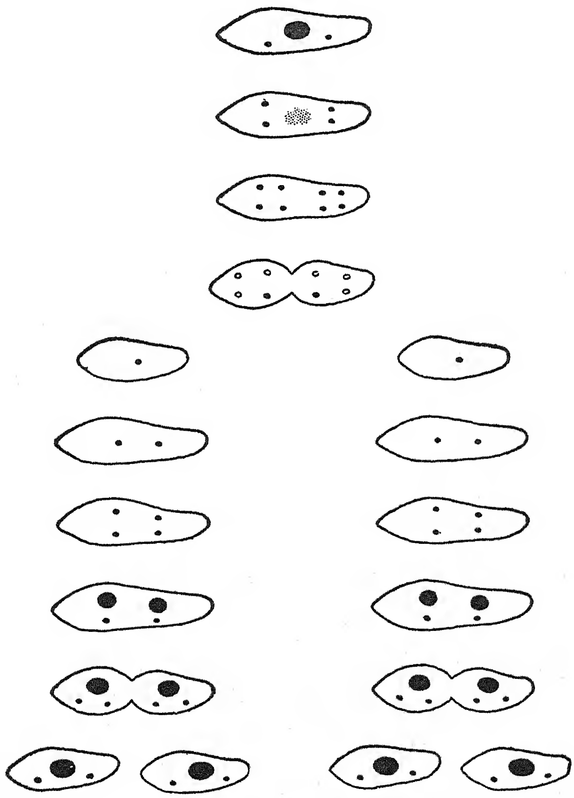


FIG. 100. Diagram of the nuclear changes during endomixis in *Paramecium aurelia*. A, typical nuclear condition; B, degeneration of macronucleus and first division of micronuclei; C, second division of micronuclei; D, degeneration of six of the eight micronuclei; E, division of the cell; F, first reconstruction micronuclear division; G, second reconstruction micronuclear division; H, transformation of two micronuclei into macronuclei; I, micronuclear and cell division; J, typical nuclear condition restored. (From Woodruff.)

lent of PARTHENOGENESIS, a type of germinal reproduction found quite commonly among the Metazoa, in which eggs undergo maturation and develop without fertilization.

SUMMARY

1. *Paramecium caudatum* belongs to the Subkingdom Protozoa and to the Phylum Infusoria, which is characterized by the presence of cilia as locomotor organelles. Several other species of the genus Paramecium are known.

2. Paramecium is considered as a "higher" type of organism than Amœba because it exhibits a higher degree of division of labor, or specialization of parts for different functions. Paramecium may be contrasted with Amœba in the following ways: it has a fixed axis with an anterior and posterior end; it has a fixed, though flexible, form; its ectoplasm is specialized to form a pellicle and a cortex; its nuclei, specialized into macro- and micronuclei, and its contractile vacuoles are anchored in fixed positions by tough strands of protoplasm; it has a fairly well-defined digestive tract with mouth, gullet, a circuit of food vacuoles, and a definite anal spot; it has fixed cilia that are coördinated in their actions by a neuromotor mechanism; its course through the water is more direct and orderly than is the more haphazard movement of Amœba; it has an alternation of generations between binary fission, an asexual phase, and conjugation, a sexual phase; its tropisms are more direct and orderly than those of Amœba; and it has specialized protective mechanism, consisting of trichocysts.

3. Binary fission involves the mitosis of the micronucleus and illustrates the mechanism of heredity in its simplest form.

4. Conjugation, with its preconjugation changes, seems to subserve two functions: that of increasing variability and that of reorganizing and thus rejuvenating the cytoplasm.

5. Reorganization of cytoplasm may be accomplished also through endomixis, which is regarded as roughly equivalent to parthenogenesis in eggs of higher organisms.

6. Paramecium is a very complex protozoan comparable in degree of complexity with a metazoan organism. The difference lies in the fact that in Paramecium differentiation of organs and systems occurs within the bounds of a single cell; it has organelles or specialized parts of the protoplasm, which have different functions, while in a metazoan organism organs composed of many cells perform the different functions of the body. Organization within the bounds of a single cell has the one main disadvantage that the size of the organism is greatly limited.

CHAPTER XVII

OTHER TYPES OF PROTOZOA

In Chapter XIII a general classification of the Subkingdom Protozoa has been given and four Phyla (Classes) of these unicellular animals have been named and characterized. Of these four phyla, we have studied in some detail representatives of only two, namely, Amœba (a member of the Phylum Rhizopoda) and Paramecium (a member of the Phylum Infusoria). We shall now briefly consider the other two phyla.

A. Phylum Mastigophora (Flagellates)

Organisms of this group occupy a peculiarly anomalous position in the world of life, for some of them are obviously plants and others as clearly animals. The botanists claim the series of colonial flagellates such as Volvox, Pandorina, Pleodorina, Eudorina, and Gonium, and classify them as a distinct family of green algæ, while almost every author of a textbook of Zoölogy deals with exactly these same organisms as colonial Protozoa. Which is right, the botanist or the zoölogist? The botanist claims these organisms because they possess chlorophyll and are able to manufacture their own food by photosynthesis, some of them possess true cell walls, some of the cells are extremely like the spores of green algæ, and the mode of reproduction is quite like that of algæ. The zoölogist claims them because, except for the fact that they possess chlorophyll, they are almost identical with certain kinds of Protozoa that are colorless and live, like animals, a dependent existence. The problem of determining to what kingdom some of the flagellate forms belong is rendered even more difficult of solution by the fact that such forms as *Chromulina* have chlorophyll and at times make their own food plant-fashion, but at other times the same individuals take in solid food in purely animal fashion. From what we have said it is evident that the separation of flagellates in such a way as to assign some to the plant kingdom and others to the animal kingdom is purely arbitrary, for here we have a large group that possesses both plant and animal character-

istics. What better classification can we give them than to consider them as belonging to a group intermediate to the two kingdoms and call them ZOÖPHYTES or PLANT-ANIMALS? It seems highly probable that from some group such as the flagellates the two present kingdoms diverged, but that some members of this generalized group have retained the primitive ancestral character of being both plant-like and animal-like at the same time.

As examples of the Mastigophora we shall briefly consider two classic types, *Euglena viridis* (an independent plant-like flagellate) and *Trypanosoma gambiense* (a parasitic flagellate causing African sleeping sickness).

1. *Euglena viridis*

Euglena (Fig. 101) has about the proportions of a rather stout cigar, with a sharp end and a blunt end. Its shape is maintained by the rather stiff ectoplasm which, however, is somewhat flexible, enabling the individual to bend and to undergo contractions and expansions of different parts of the body. Peristaltic waves of contraction at times sweep over the whole body, a behavior termed euglenoid movement. The surface of the body is characterized by spiral sculpturings which may aid in the spiral path through the water. In locomotion the blunt end goes forward and the sharp end is in the rear, an example of good stream lining. At the front end is the locomotor organ, a long FLAGELLUM which protrudes from the gullet. The flagellum is far from simple for it is composed of an axial filament covered by a sheath attached deep in the endoplasm. At one side of the gullet is a RESERVOIR, surrounded by many small contractile vacuoles emptying into it. Its rôle is doubtless the same as that of contractile vacuoles in other protozoans. Near the reservoir is a small red spot, the EYE-SPOT, which may be a primitive eye in the sense that it is sensitive to light.

In the center of the endoplasm is the single spherical nucleus. The rest of the endoplasm is packed with green CHLOROPLASTS and peculiar rod-shaped bodies called PARAMYLIUM BODIES, which are similar to starch grains and doubtless play the rôle of food storage.

Euglena impresses one as being a bit greedy, for, although it can make its own food like a green plant, it is not satisfied with this simple diet, but must needs at the same time feed on small

organisms such as bacteria. These particles are drawn to the gullet through the vortex-like suction of the flagellum and are carried down the gullet in such a way as to form FOOD VACUOLES like those of Paramecium.

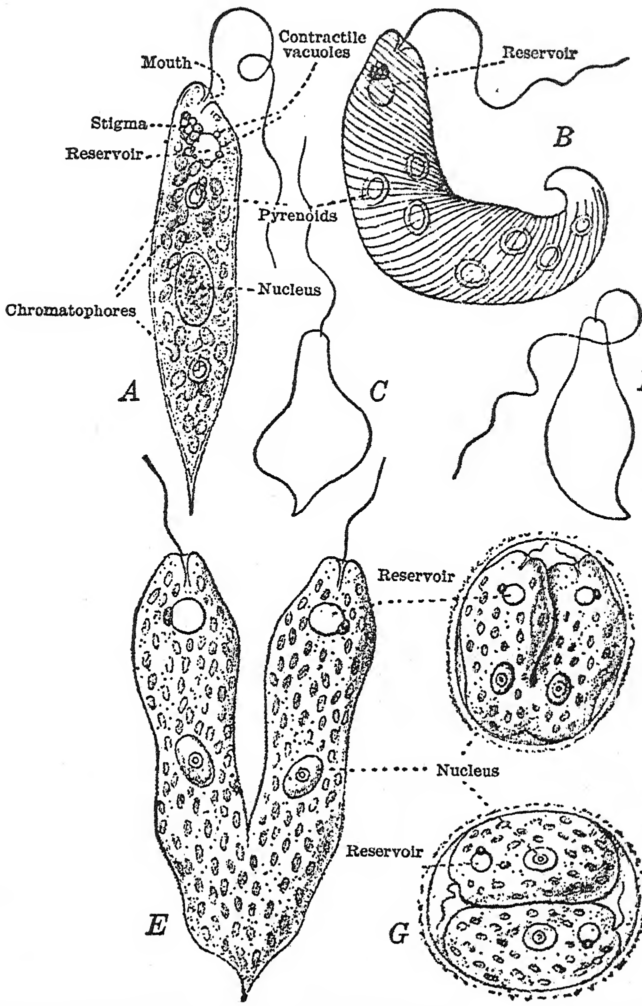


FIG. 101. *Euglena viridis*. *A*, view of free-swimming specimen showing details of structure; *B*, another animal showing change of shape and striations; *C* and *D*, outlines showing stages of contraction; *E*, reproduction by longitudinal fission; *F* and *G*, division within a cyst. (*A–D*, from Bourne; *E–G*, from Bourne, after Stein.)

Many experiments on animal behavior have been conducted with Euglena and it exhibits much the same tropisms as those described for Amœba and Paramecium.

The **life cycle and reproduction** of Euglena involve an ACTIVE PHASE and an ENCYSTED PHASE (Fig. 101, *F*). During the active phase division takes place by longitudinal (occasionally transverse) fission (Fig. 101, *E*). On rare occasions two individuals, which may be considered as gametes, come together side by side and fuse permanently (not like the temporary conjugation in Paramecium) to form a zygote. At any time when the food or other conditions become unfavorable the individuals round up, secrete a thick coating about the body and form cysts. While encysted they may or may not undergo fission. When conditions become favorable again they emerge from the cyst and resume the active phase. Some forms, extremely similar to Euglena, lack chlorophyll altogether and live purely as animals. The single members of colonies of Volvox and its relatives are very much like Euglena, for they possess similar reservoirs and red eyespots. Hence it seems impossible to avoid the conclusion that the two groups are related.

2. *Trypanosoma gambiense*

This well-known parasite of animals and man has become famous in the annals of medicine because it is the parasite responsible for Gambian sleeping sickness. We shall here dwell chiefly on the medical aspects of its life and shall give but scant attention to the details of its structure. Figure 102 shows the general appearance of several common species of trypanosomes.

In form it is spindle-shaped, with a single long flagellum at one end and an undulating membrane running lengthwise of the body. It has a single nucleus. It lacks the stiff ectoplasm of Euglena and is thus able to absorb nutriment through the surface membrane.

In the human being Trypanosoma is at first a blood parasite, but in final stages it invades the cerebro-spinal fluid of its victims and through the toxins it produces brings on the typical symptoms of the disease, a profound sleep that usually ends in death. The disease is transmitted by means of a blood-sucking fly, the TSETSE FLY (Fig. 175, A), which takes in the parasite with the blood sucked in as food. The organism multiplies in the intestine of the fly, invades its salivary glands and is transferred to another human

victim by the bite of the insect. The parasite also invades the blood stream of the larger African animals, through bites of the same fly, but does not produce in them any very serious symptoms. On the other hand, these animals act as carriers of the

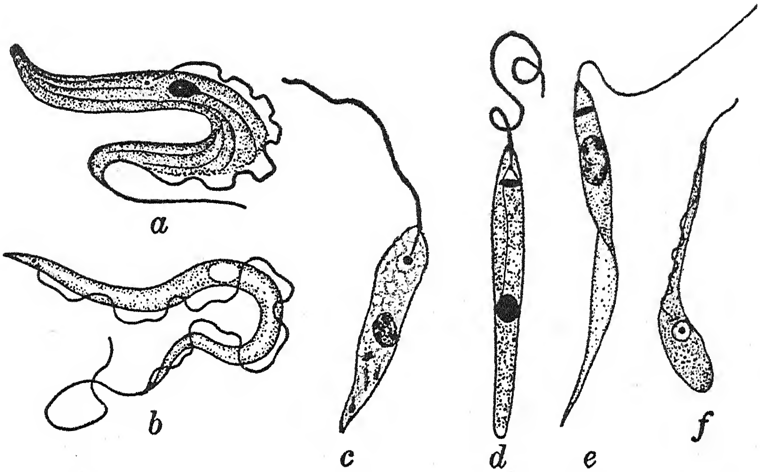


FIG. 102. Several kinds of trypanosomes. *a, Trypanosoma rotatorium,* from the frog. *b, Trypanosoma diemyctyli,* from the newt. *c, Leishmania donovani,* from man. *d, Herpetomonas muscarum,* from the house fly. *e, Phytomonas elmassiani,* from the milkweed plant. *f, Crithidia gerridis,* from the water strider. (From Hegner, after various authors.)

disease and man can receive the infection from these carriers through the medium of the tsetse fly, which bites both man and beast.

This type of life cycle is characteristic of many serious disease-producing Protozoa and in later chapters further attention will be paid to this phenomenon.

B. Phylum Sporozoa

This whole group, in contrast with other phyla of Protozoa, includes only parasites. The name of the group is derived from the fact that the most conspicuous phase of the life cycle involves the production of spores, minute reproductive cells. The group is a large and varied one, but perhaps the best known example is a species of *Monocystis* (Fig. 103), which is nearly always found parasitic in the seminal vesicles of earthworms. The full-grown

individual is an elongated, somewhat wormlike organism with a single nucleus. It moves about slowly with a wriggling motion. In earlier stages of its life cycle it lives within the cells of the host

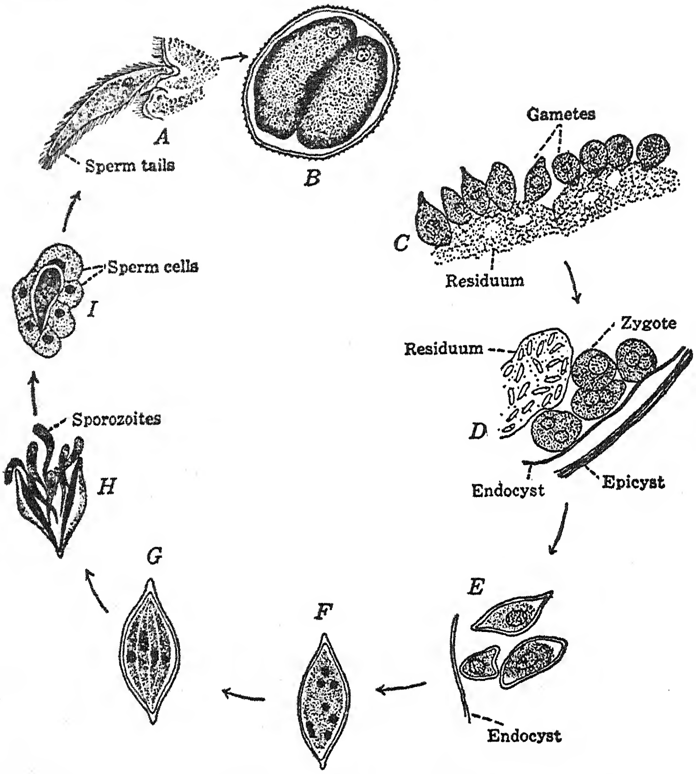


FIG. 103. Life cycle of a sporozoan. *Monocystis*, parasitic in the seminal vesicle of the earthworm. *A*, a mature individual attached to the sperm-funnel of the earthworm. *B*, two mature individuals joined side by side. *C*, gametes formed within the cyst. *D*, conjugation of gametes to form zygotes. *E*, zygotes that have become spores. *F*, a single spore containing eight nuclei. *G*, a fully developed spore containing eight sporozoites. *H*, the eight sporozoites escaping from the sporocyst. *I*, young trophozoite among sperm-mother cells. (From Hegner, after various authors.)

tissues, but later penetrates the cell membrane and comes to lie free in the cavity of the seminal vesicle, where it finds a rich supply of nutriment which it absorbs through its own thin external membrane. It grows rapidly there and acquires a store of nutriment to be used during the long period of encystment. During

this latter period repeated divisions of the nucleus occur and ultimately numerous gametes are produced, each with its own nucleus. The gametes, which are indistinguishable as to sex, unite in pairs to form zygotes, each of the latter secreting about itself a spindle-shaped spore case made of resistant material. In this stage the "spore" may be transferred to another earthworm during copulation, and the life cycle is started over in another host animal. It is rare to find an adult earthworm free from this parasite. The whole life cycle is shown in Figure 103.

SUMMARY

1. The members of the Phylum Mastigophora of the Subkingdom Protozoa are characterized by having one or a few long flagella as locomotor organs.
2. The phylum seems to belong partly to the Plant Kingdom and partly to the Animal Kingdom; hence the group might be called Zoöphyta, which means plant-animals.
3. *Euglena viridis*, a common type for laboratory work, has both animal-like and plant-like modes of nutrition, for it feeds on bacteria, etc., and also carries on photosynthesis.
4. *Trypanosoma gambiense* is an example of Mastigophora that are animal parasites. This particular species is the cause of African sleeping sickness. It carries on part of its life history in the body of the tsetse fly and the rest in the tissues of man or ungulates.
5. The Phylum sporozoa of the Subkingdom Protozoa consists exclusively of parasitic Protozoa that live in the tissues of higher animals. They are chiefly characterized by a conspicuous spore-producing stage in their complex life history.
6. *Monocystis*, a genus of sporozoans parasitic in the seminal vesicles of earthworms, is a classic type. Its life cycle is shown in Figure 103 and need not be studied in detail.

CHAPTER XVIII

PROTOZOA AND METAZOA

A. Theories as to the Interrelationships of the Two Subkingdoms

In Chapter V we have already discussed the question of various levels of life units and have adopted the view that Protozoa represent individuals at the unicellular level of organization. In Chapter XIV we presented the opinion of the protozoölogist, Clifford Dobell, that an animal such as a Paramecium is not merely the equivalent of one of the millions of cells in the body of a man or a worm, but is in one sense equivalent to the whole body of such forms. Dobell considers it misleading to consider Protozoa as unicellular individuals, preferring to regard them as noncellular, since they attain a high degree of complexity without dividing their material up into many cells.

The more familiar view about the Protozoa is that they constitute a primitive group of organisms that are truly one-celled in their organization, that the more complex types have been derived from much more primitive ancestors which had both plant and animal characters, and that from this primitive ancestral group were also derived the first Metazoa, the ancestors of present Metazoa.

The theory that the Metazoa have had a protozoan ancestry is now generally accepted, though the opposite view has occasionally been expressed, that modern Protozoa (or at least some of them) have been derived from Metazoa by simply omitting the multicellular phase from their life cycle. This somewhat bizarre theory implies that the protozoan individual is simply a germ cell of some metazoan that lives a life of its own, getting its own food and playing the rôle in nature of an individual. When it divides to initiate the multicellular state the two daughter cells break loose from each other and become separate individuals instead of helping to build up a multicellular individual. The view that a protozoan is equivalent to a germ cell that never gets over being a germ cell, is supported by the fact that sometimes two individual pro-

tozoans fuse to form the equivalent of a zygote (fertilized egg). Indeed in some Protozoa large stationary individuals (like eggs) fuse with small motile individuals (like sperms), and produce fusion individuals (zygotes). This theory, that Protozoa are degenerate derivatives of Metazoa, while not unreasonable in some respects, is so improbable that we shall not give it further consideration.

The Theory that Metazoa Have Evolved from Protozoa.—As already intimated, this is the orthodox view as to the relationship between Metazoa and Protozoa. The evidences favoring this theory are mainly of two sorts: *a*, there exist a number of kinds of Protozoa that constitute a series ranging from those that form temporary multicellular aggregates to those forming well-defined colonies that seem to be on the verge of becoming multicellular units of a higher order, or true Metazoa; *b*, in the life history of a metazoan organism the individual passes through the one-celled stage (the egg or zygote), passes through stages (called cleavage stages) which are like some of the simpler aggregates of Protozoa, and later attains the state of being a hollow sphere of cells arranged in a single layer (the blastula stage) at which time it is often compared to a colony of flagellates such as Volvox. Beyond this level the parallelism ceases. In these two types of evidence we have an example of the kinds of evidence the biologist customarily makes use of in attempting to discover relationships between two groups of animals, the one suspected of being ancestral to the other. He looks over the whole range of types belonging to the lower group in an effort to find tendencies leading toward the typical condition found in the higher group, and then he surveys the higher group looking for conditions that are similar to or reminiscent of those of the lower group. He also hopes to find connecting-link types, with characters intermediate between the higher and lower group. It is natural to expect to find among the early embryonic stages of the higher group greater resemblances to the lower group than are present in the advanced developmental stages. This expectation is so frequently realized that it has come to be believed that the developmental stages of a higher type of animal tend to pass through conditions that are in a general way equivalent to the series of ancestral types from which it has been derived. This statement is a paraphrase of the LAW OF RECAPITULATION, or the BIOGENETIC LAW, about which more will be said in a later connection.

B. Possible Protozoan Ancestors of Metazoa

Accepting the view that Metazoa have probably been derived from protozoan ancestors, we may now ask ourselves what particular group of Protozoa seem most likely to be ancestral to Metazoa. The one group that seems best suited for this purpose is the PHYLUM (CLASS) MASTIGOPHORA, or flagellates. We have in Chapter XVII pointed out that members of this group are classed as both animals and plants and might well be called plant-animals. The reasons for selecting the flagellates rather than one of the other protozoan groups as hypothetical ancestors to Metazoa are, first, that the flagellates show a type of colony formation that approaches close to the metazoan condition, and, second, that the lowest of the metazoan phyla (Porifera and Cœlenterata) have cells in parts of their bodies that are strikingly similar to flagellates. We shall in subsequent chapters discuss the collar-flagellate cells lining the water passages of sponges, and the flagellate cells lining the digestive tract of Hydra and its relatives.

The Volvox Series

The best series of stages leading from isolated unicellular organisms to well-defined multicellular colonies is found in members of the family Volvocales, which are commonly classed as plants but are sometimes appropriated by zoölogists to help them bridge the gap between Protozoa and Metazoa. If we bear in mind that no claim is made that this series is in any sense the actual ancestral series through which the Metazoa are supposed to have come, but that the series merely shows a line of progress of which flagellates are capable, we need not worry seriously as to whether these organisms are more properly plants than animals, or *vice versa.*

The simplest member of the family is *Chlamydomonas* (Fig. 104, *b*), which like most Protozoa is noncolonial. The single-celled body is oval in shape, has two flagella, a green chromatophore, two contractile vacuoles, a red eye-spot, and a cell wall similar to that of unicellular plants. One sees in this list of characters some plant-like and some animal-like features. Reproduction takes place by binary fission and the two daughter cells immediately separate and become two individuals. Sometimes two similar individuals (isogametes) fuse together to form a zygote.

A simple colonial type is found in *Gonium pectorale* (Fig. 105), which divides four times to form a colony of sixteen cells, each of which is like the whole individual of Chlamydomonas in the de-

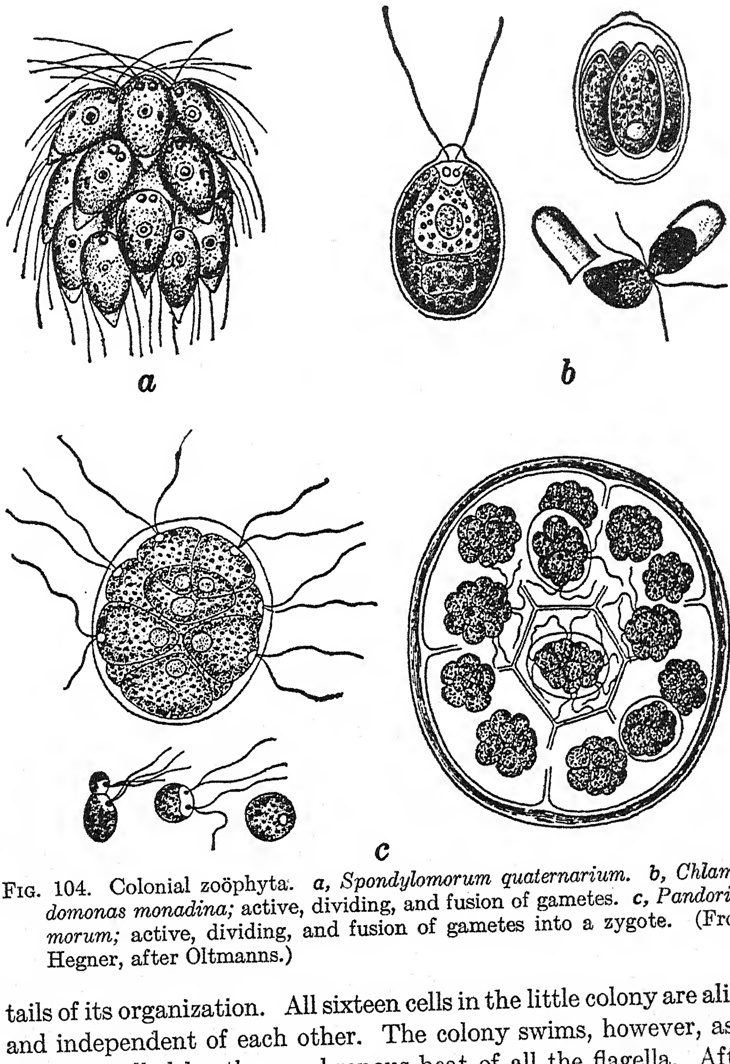


FIG. 104. Colonial zoöphyta. *a, Spondylomorum quaternarium.* *b, Chlamydomonas monadina;* active, dividing, and fusion of gametes. *c, Pandorina morum;* active, dividing, and fusion of gametes into a zygote. (From Hegner, after Oltmanns.)

tails of its organization. All sixteen cells in the little colony are alike and independent of each other. The colony swims, however, as a unit, propelled by the synchronous beat of all the flagella. After a time each of the sixteen cells divides and redivides to form daughter colonies of sixteen cells, which part company, and each

colony grows up to be as large as the parent colony. Sooner or later the cells in the colony separate to become ISOGAMETES, and these fuse to form zygotes, from which new colonies start. Another species of Gonium differs from the one described in having smaller colonies of four cells, but in other respects is the same.

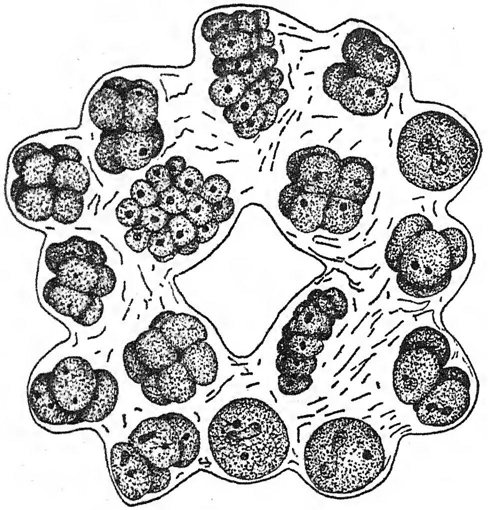


FIG. 105. Reproduction of *Gonium pectorale*. Each of the sixteen cells of the ordinary colony divides until a sixteen-cell stage results; the old colony then breaks up and the sixteen young colonies grow independently. (From Calkins.)

Pandorina morum (Fig. 104, *c*) is a species with a more compact type of colony, composed of eight or sixteen cells bound together in a common gelatinous envelope. All the cells are alike, with two flagella, one contractile vacuole, and a red eye-spot. As in Gonium, there must be some slight integration of the individual cells, for their cilia beat in a coördinated fashion. All the cells, however, are alike in appearance and function. Each cell is potentially a germ cell, for each divides and forms a colony like the parent colony. This mode of reproduction is continued for several generations, but in a final generation all the cells of the colony separate to form gametes, which in this case are described as ANISOGAMETES (in which larger and smaller gametes are distinguishable), and these fuse, a larger with a smaller, to form zygotes, from which new colonies arise (Fig. 104, *c*, left).

Eudorina elegans is very similar to Pandorina, differing in that sometimes as many as thirty-two or more cells make up a colony. In this species the gametes are quite definitely anisogametes. Moreover, the macrogametes (eggs) arise in one colony and the microgametes (sperms) arise in another. In the series described up to this point it is important to note that all cells are with-

out exception potentially germ cells, there being no body cells (somatic cells).

Pleodorina illinoisensis is similar to the two previously described species in all respects except that it forms colonies of thirty-two cells, only twenty-eight of which are germ cells, capable of reproducing new colonies or forming anisogametes. The remaining four cells are distinguished by their smaller size and may be regarded as constituting the first beginnings of the SOMA, or body, as distinguished from germ cells. In an allied species, *P. californica*, larger colonies of sixty-four or one-hundred and twenty-eight cells are produced, about half of which are somatic cells. So in this genus we have the introduction of the important specialization of somatic and germinal cells.

Volvox globator (Fig. 106) is a classic in biology, used by both zoölogists and botanists to illustrate the transition from unicellular to multicellular life units. A Volvox colony, or individual as some prefer to call it, consists of several thousands of cells, each of which, like the cells of the other members of the family, has two flagella, a chloroplast, a contractile vacuole, and a red eyespot. The numerous cells of the colony are arranged in a single layer on the outside of a relatively large sphere the interior of which is filled with a watery fluid. Each cell proper is inclosed in a coating of gelatinous material and these coats are packed against each other so as to give the surface a honey-comb appearance due to the hexagonal outline of the masses. Each cell is connected with six neighboring cells by as many protoplasmic bridges, which doubtless serve to put all the cells into communication with one another, making coördinated action possible. All but a few of the cells are regarded as somatic cells, for they do not reproduce new individuals. Some observers have claimed that they have noted the beginnings of differentiation of cells among the somatic cells. According to an unpublished account by ***L. H. Hyman***, Volvox revolves on an axis, and in forward locomotion travels with one pole of the axis always ahead. The claim is made that a considerable number of cells at the forward pole have larger eyespots than have the other cells. If these accounts can be trusted, and we believe they can be, Volvox takes an important step toward differentiation of the somatic cells. One step further and it would undoubtedly be a multicellular individual instead of a rather tightly integrated colonial protozoan (or protophyte).

Volvox also shows further steps in the differentiation of germ cells As we have said, a few of the surface cells are germinal although the majority are somatic. These germinal cells lose their flagella and their protoplasmic connections with adjacent cells, grow large and spherical, and drop from the surface into the fluid center of the colony. Some of them, called PARTHENOGONIDIA,

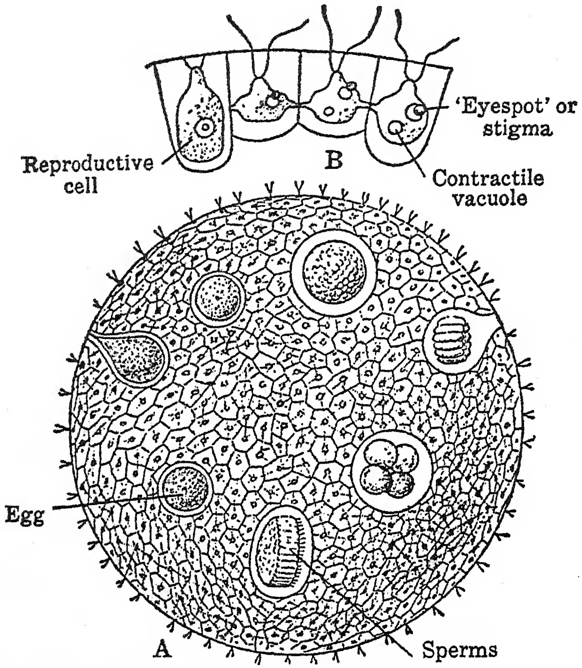


FIG. 106. *Volvox globator.* A, whole colony, showing vegetative individuals, eggs, sperms and young colonies. B, a few surface individuals one of which is enlarging to form a reproductive cell. (After Woodruff.)

are similar to some of the cells of a Pandorina colony in that they simply divide to form new colonies without fusing with other cells to form zygotes. The other germinal cells are of two kinds. One kind does not divide but remains large and spherical, thus constituting a MACROGAMETE or egg; the other kind divides and redivides many times to form a flattened bundle of elongated cells, the whole resembling a bundle of cigars, each cell of which is a MICROGAMETE (sperm) with two flagella. A sperm swims to an egg and fuses with it to form a ZYGOTE, which secretes a spiny coat of pro-

tective material about itself. In this encysted form the zygote is able to carry the species over the winter or through a period of drought. When favorable conditions return the cyst is ruptured, permitting the zygote to emerge and to divide and thus to begin the formation of a new colony. One interesting fact about a mature colony of Volvox that should be emphasized is that, after a period of reproduction, during which the central part of the sphere has become filled with new colonies or zygotes, the original sphere ruptures, releasing the new colonies or zygotes, and then

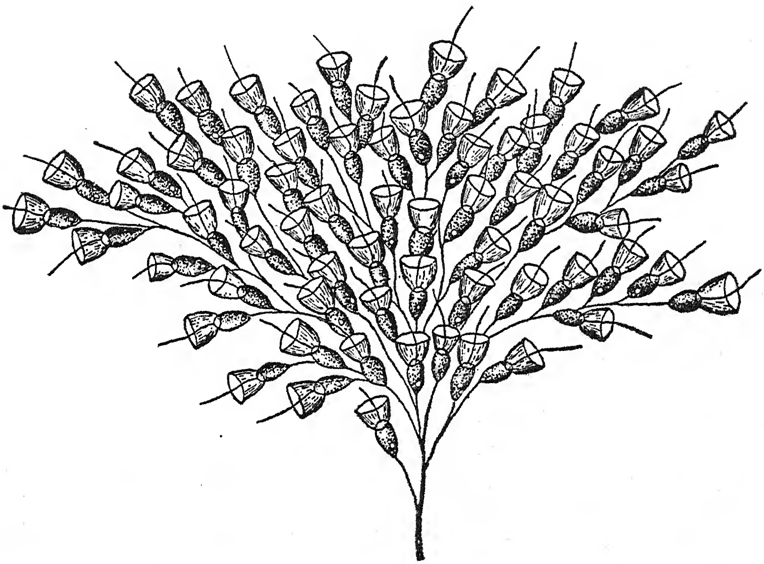


FIG. 107. An arboreal colony of flagellated protozoa, *Codosiga cymosa*. (From Calkins, after Kent.)

dies. This is in contrast with the condition found in some of the earlier members of the series in which all the cells live on, except for accidental death, to form new colonies or zygotes. In Volvox and its allies we have the first case of natural death among the Protista, for the parent body dies and only the germ cells are potentially immortal.

Viewed critically, this series of transitional stages between units at the unicellular level and those at the multicellular level illustrates merely one possible path of evolution within a group now living, a group that must not be considered as the actual series of

Volvox also shows further steps in the differentiation of germ cells As we have said, a few of the surface cells are germinal although the majority are somatic. These germinal cells lose their flagella and their protoplasmic connections with adjacent cells, grow large and spherical, and drop from the surface into the fluid center of the colony. Some of them, called PARTHENOGONIDIA,

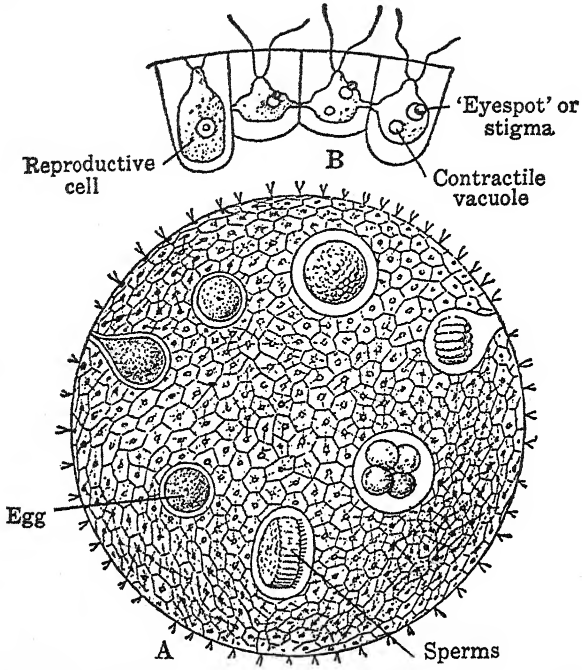


FIG. 106. *Volvox globator.* A, whole colony, showing vegetative individuals, eggs, sperms and young colonies. B, a few surface individuals one of which is enlarging to form a reproductive cell. (After Woodruff.)

are similar to some of the cells of a Pandorina colony in that they simply divide to form new colonies without fusing with other cells to form zygotes. The other germinal cells are of two kinds. One kind does not divide but remains large and spherical, thus constituting a MACROGAMETE or egg; the other kind divides and redivides many times to form a flattened bundle of elongated cells, the whole resembling a bundle of cigars, each cell of which is a MICROGAMETE (sperm) with two flagella. A sperm swims to an egg and fuses with it to form a ZYGOTE, which secretes a spiny coat of pro-

tective material about itself. In this encysted form the zygote is able to carry the species over the winter or through a period of drought. When favorable conditions return the cyst is ruptured, permitting the zygote to emerge and to divide and thus to begin the formation of a new colony. One interesting fact about a mature colony of Volvox that should be emphasized is that, after a period of reproduction, during which the central part of the sphere has become filled with new colonies or zygotes, the original sphere ruptures, releasing the new colonies or zygotes, and then

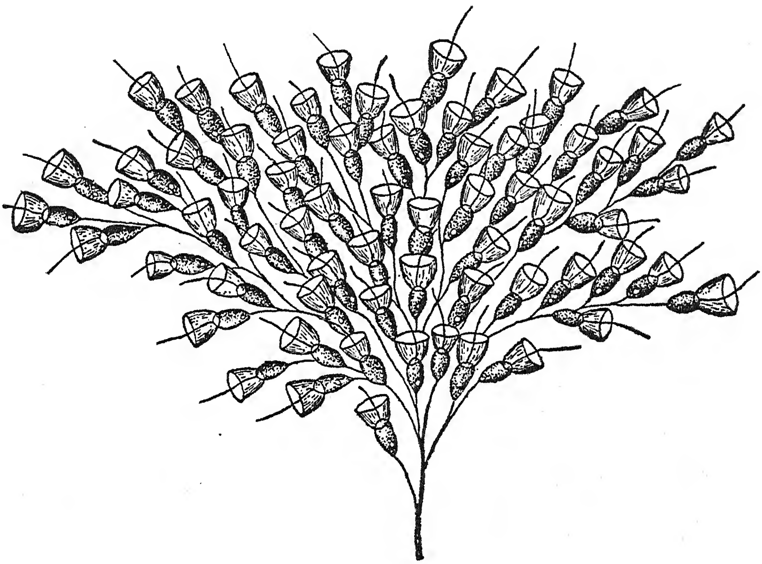


FIG. 107. An arboreal colony of flagellated protozoa, *Codosiga cymosa*. (From Calkins, after Kent.)

dies. This is in contrast with the condition found in some of the earlier members of the series in which all the cells live on, except for accidental death, to form new colonies or zygotes. In Volvox and its allies we have the first case of natural death among the Protista, for the parent body dies and only the germ cells are potentially immortal.

Viewed critically, this series of transitional stages between units at the unicellular level and those at the multicellular level illustrates merely one possible path of evolution within a group now living, a group that must not be considered as the actual series of

ancestral types that have given rise to Metazoa. The fact that all the Volvocales are provided with chlorophyll and have cell walls like plant cells precludes the possibility that they themselves could be really ancestral to any animal group. It seems reasonable, however, to regard this series as illustrating the stages through which the real ancestors of the Metazoa may have passed in reaching their present status.

Among the unquestioned Protozoa, which are surely animals and not plants, we have many colonial types that to some extent help to bridge the gap between Protozoa and Metazoa, but there is no series so nicely graded as the Volvocales and there is no type that so nearly approaches the metazoan condition as Volvox. Nearly all of the true protozoan colonials form rather loosely integrated colonies of the arboroid or branching type (Fig. 107), a form ill suited to giving rise to the compact metazoan body. It seems probable that those ancestral Protozoa that formed colonies of the compact type that could lead to the metazoan condition have long ago given rise to Metazoa and thus ceased to exist as colonial Protozoa.

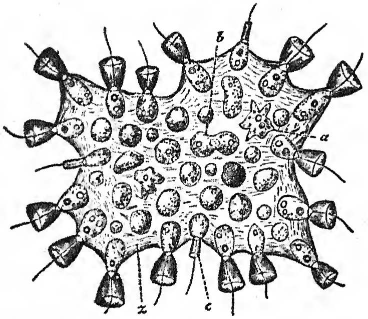


FIG. 108. *Proterospongia hæckeli*, a colonial CHOANOFLAGELLATE. *a*, amœboid cell; *b*, a cell dividing; *c*, cell with small collar; *z*, jelly. (From the Cambridge Natural History, after Kent.)

One type of colonial protozoan now living has a compact body form of the kind needed to lead to the metazoan condition. This type is known as *Proterospongia* (Fig. 108). This species forms more or less globular colonies of cells all imbedded in a common gelatinous matrix secreted by the cells themselves. The cells at the surface are typical collar-flagellate cells, similar to those of many other Protozoa. The collar, a delicate funnel of modified protoplasm, surrounds a single flagellum which whips food particles into the collar and down into the body of the cell, where they are digested. The central part of the colony is occupied by amœboid cells that wander about by pseudopodial locomotion, getting food from the collar cells, dividing to form more cells and thus increasing the size of the colony, or acting as germ cells to start new col-

onies. This looks like a differentiation of somatic and germinal cells, but is not truly such, for the collar cells at intervals withdraw their collars and flagella and wander inward to become amœboid cells, while the latter come to the surface to form collar cells. Thus the differentiation between soma and germ is only temporary. We shall have occasion to refer once more to Proterospongia in Chapter XIX, when the phylogenetic relationships of the sponges are discussed. No other protozoan group seems to show at present any type of colonial aggregation leading in a metazoan direction. As has been intimated, it seems probable that those groups with metazoan capacities have long ago realized them.

C. Protozoa and Metazoa Compared and Contrasted

In both subkingdoms the life cycle consists of alternate phases of vegetative activity and reproductive activity. In the vegetative phase rapid cell division results from the expropriation of abundant new energy and resultant growth. Then comes a phase characterized by cessation of growth and by reproduction of new individuals.

In the Protozoa the two phases are not always clearly defined, for the period of active metabolism accompanied by growth and cell division also involves the reproduction of new individuals, resulting from the separation of the division products. Even in such forms, however, a period of fission, as in Paramecium, alternates with a period of conjugation. In other words, a period of asexual reproduction (which is equivalent to cleavage and development in a metazoan) alternates with a period of gamete formation, and hence sexual reproduction.

As is readily seen, the essential difference between Protozoa and Metazoa, from this point of view, lies in the fact that in the vegetative phase the Protozoa typically produce separate unicellular individuals, while in the Metazoa the daughter cells remain together to form many-celled masses that become multicellular individuals.

All the Metazoa exhibit anisogamy (differentiation of gametes) in an extreme form and they all reproduce sexually, though many of them have adopted various asexual methods of reproduction that will be discussed in Chapter XLIII.

The most important step which the Metazoa have taken beyond anything found in Protozoa, or even in the Volvox series, is the differentiation of somatic cells for different functions, or the intro-

duction of division of labor among body cells. So far as their reproductive specializations are concerned, the Metazoa and Protozoa are practically on a par. Hence it is only in the vegetative phase of the life cycle that the Metazoa have advanced beyond the Protozoa. They have carried the differentiation of the soma to great lengths, producing large and complex multicellular bodies.

SUMMARY

1. In spite of the contrary view that some Protozoa may be degenerate descendants of Metazoa, it is generally accepted that Protozoa are ancestral to Metazoa.
2. Evidences for the protozoan origin of Metazoa are: the existence of a series of cellular aggregates and colonial Zoöphyta that almost bridges the gap between the two subkingdoms; the fact that all Metazoa begin their life cycle with the one-celled stage (the zygote); and that they pass through stages roughly equivalent to cell aggregates and colonial Protozoa, thus illustrating the Biogenetic Law.
3. The Volvox series of simple and colonial Mastigophora shows how in one group a series of transitions from the one-celled type of individuality to the many-celled type of individuality may have been attained.
4. A special study of Volvox illustrates the various modes of reproduction found among Protozoa.
5. In a statement contrasting Protozoa with Metazoa, it is pointed out that the main advance in the latter over the former consists of the differentiation of the body tissues (the soma) for different functions.

CHAPTER XIX

SPONGES

(PHYLUM PORIFERA)

A. General Characteristics

Even though they fail to meet the popular criteria of what animals ought to be, sponges are truly animals. In the adult state they are sessile organisms, fastened down for life to rocks, shells, or wharf piles, and therefore incapable of moving about as one expects animals to do. They do not visibly respond by movements when touched, and they display no other signs of animation under casual observation. Why then do we insist that they *are* animals?

In the first place, they are made up of living cells, usually many thousands of them, each in itself a characteristic animal cell. Moreover, these cells are arranged in definite layers and differ from one another structurally and functionally in accord with the position they occupy in the individual. A sponge then is a real organism, an individual in the technical sense, but its organization is loose and the interdependence of part upon part is relatively slight. An example of a simple sponge is *Leucosolenia* (Fig. 109), a species common along the New England coast. Individuals of this species grow in colonies or clusters, and reach a length of about one inch. Each sponge looks like a little slender urn or flask with the bottom fastened to the substratum and the mouth uncorked. This opening is not a real mouth in the sense that it is the portal for the entrance of food, yet it is called the osculum (meaning little mouth). Nothing enters the body through the osculum. On the contrary, it acts

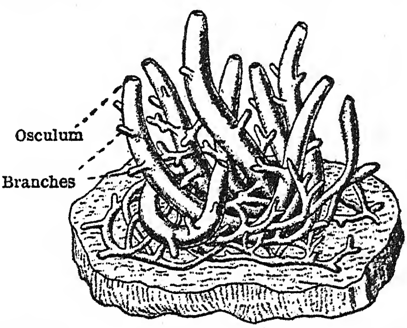


Fig. 109. A small colony of *Leucosolenia*, a simple sponge. (From Lankester.)

as an exit for water and wastes. The mouths of the sponge are myriad, consisting of countless little INCURRENT PORES (OSTIA) that dot the whole external surface. It is the presence of these pores that gives the name "Porifera" to the phylum.

An animal with hundreds of mouths cannot be thought of as very highly organized, for there is no well-defined apical region and no single gradient. That a sponge is in truth loosely organized is shown by the fact that if an individual be torn to fragments and these be strained through the meshes of closely woven silk fabric, the various kinds of cells will be separated one from another. In spite of this complete breaking down of organization, the cells can go on living separately and are able to aggregate into small bunches or masses out of which new sponges arise. These and other considerations have led to the conclusion that sponges are hardly entitled to full rank as Metazoa, but are only slightly more advanced than some of the more elaborate colonies of Protozoa. They differ from protozoan colonies, however, in the fact that definite tissues are differentiated, including a protective external tissue, an internal nutritive tissue, and an intermediate tissue that contains skeletal cells, reproductive cells, and some cells that assist in nutrition. There are also muscular tissues associated with the openings of pores and passageways, and these serve to regulate the flow of water through the body. Because the Porifera are multicellular organisms, but lack suf-

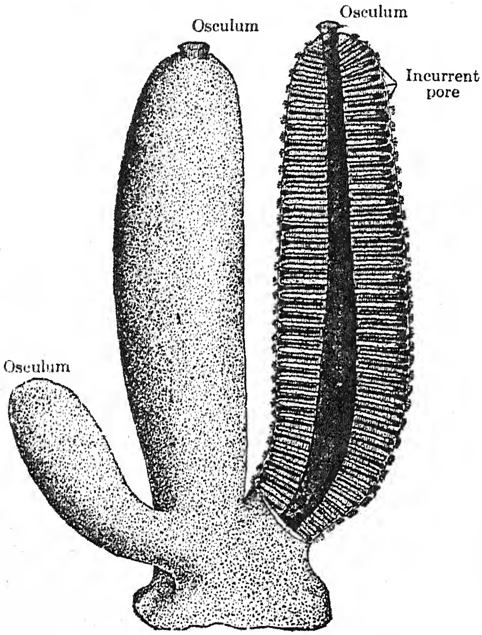


FIG. 110. A typical sponge, *Sycon*. The right-hand individual is shown in longitudinal section. (From Parker and Haswell.)

ficiently definite organization to be considered true Metazoa, they have been assigned by some biologists to a separate division of the Subkingdom Metazoa, the PARAZOA.

B. THE ANATOMICAL PLAN OF A SPONGE

If one cut open a sycon sponge, such as that shown in Figure 110, and examine it under the low power of the microscope, he will find it a rather definite labyrinth of canals or passageways. In the center is a large cavity, the CENTRAL CAVITY, which is in no sense comparable to a stomach or intestine. Radiating from this cavity and in communication with it are numerous canals (EXCURRENT CANALS) that end blindly near the surface (Fig. 111). Between the excurrent canals are similar canals (INCURRENT CANALS), each opening to the outside by a pore (incurrent pore, or OSTIUM) and ending blindly near the central cavity. Numerous tiny passages (PROSOPYLES) place the incurrent canals in communication with the excurrent canals, so that it is possible for currents of water to pass from the surface into the central cavity. The incurrent canals are apparently merely water conduits, for they are lined with flat pavement cells without other function than that of furnishing a firm, smooth surface.

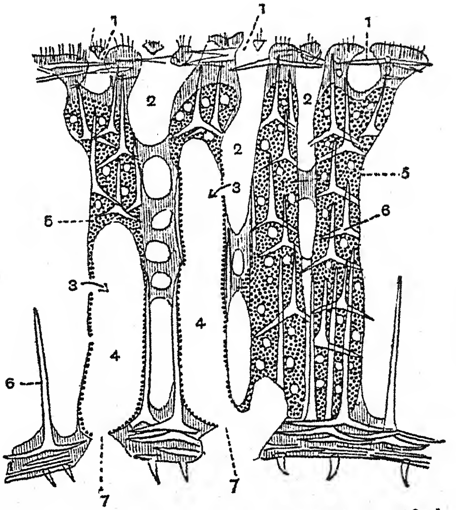


FIG. 111. Section of *Grantia*, highly magnified, showing:—1, openings of incurrent canals; 2, incurrent canal; 3, prosopyles; 4, excurrent canal; 5, collar cells; 6, spicules; 7, openings of excurrent canals. (From Dendy.)

The cells lining the excurrent canals, however, are very different. Each cell is provided with a funnel, or collar, opening at the surface and a flagellum, or animated whip, which lashes water and suspended food particles into the cell mouth at the base of the collar (Fig. 112). These then are the food-capturing cells of the sponge.

Small nutritive particles are taken into the cell protoplasm, digested, and part of the nutrition passed on to deeper lying cells. The combined movements of the flagella, or whips, are in such a direction that water currents are created toward the central cavity. This is the whole mechanism of water flow, the only superficial sign of life in the sponge. The central cavity is merely a common conduit for conducting to the outside the water expelled from the excurrent canals. The current may be checked by contracting the muscle cells surrounding the incurrent pores.

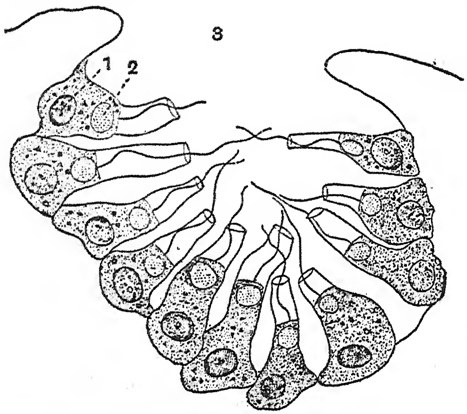


FIG. 112. Section of portion of excurrent canal, highly magnified, showing collar cells and flagella. 1, nucleus; 2, vacuole; 3, opening into central cavity. (From Shipley and MacBride.)

It is to be noted that all digestion is INTRACELLULAR, that is, within the individual cell bodies. Similarly, respiration and excretion are carried out by each and every cell; for there are no special tissues for these functions.

The external surface of a sponge is covered by a layer of relatively tough protoplasm in which occur many nuclei. Such a layer, with no distinct cell boundaries but with numerous nuclei, is known as a SYNCYTIUM.

Since the living tissues of the sponge are in themselves quite soft, and since the whole life of the animal depends upon the maintenance of a more or less constant form with open passageways for the water circulation, a supporting framework is highly essential. Throughout the deeper layers of the body there is an intricate trestlework composed of calcareous rods and other, more complex units. These may be composed of rods fused together into symmetrical forms, some being shaped like a T, others not unlike the little iron "jacks" used in the favorite game of schoolgirls. These SPICULES, as they are called, constitute the skeleton of the sponge and serve to keep the water passages from collapsing.

Compound sponges of various grades of complexity are essentially of no higher level of organization than the simpler types just described, for they are merely like an apartment building composed of repeated units, each like the rest. If we think of the Leucosolenia type of sponge as a single apartment we may properly designate compound sponges apartment buildings of varying degrees of size and complexity. Some of the stages of increasing complexity are shown in Figure 113.

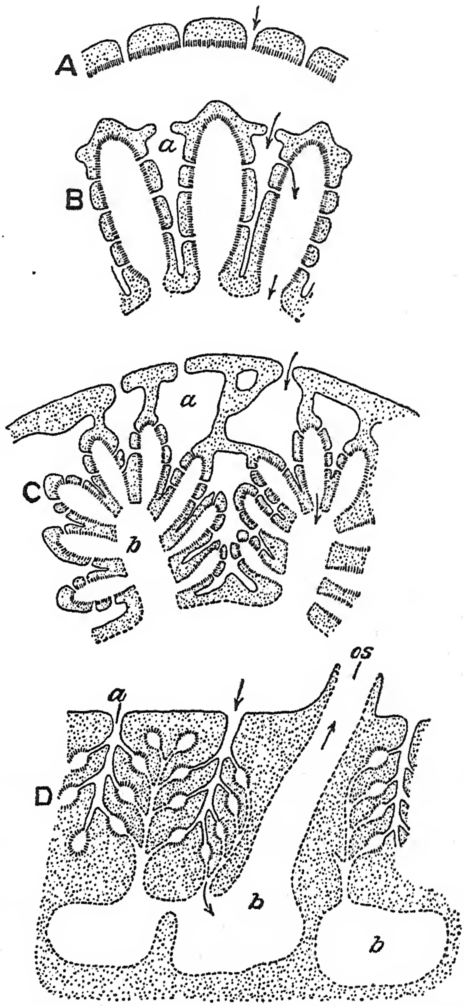


FIG. 113. Diagram of the canal system of various sponges. A, section through part of wall of simplest type; B, section through wall of Ascon type, e.g., *Grantia;* C, section through wall of a complex sponge which is constructed like a colony of Grantias; D, longitudinal section through a portion of a specialized type of sponge with small, restricted flagellated chambers. *a*, incurrent canals; *b*, central cavities; *os*, osculum. (From Parker and Haswell.)

The various subclasses, orders, and families of sponges differ rather sharply from one another in the materials used for the skeleton and in the shape of the skeletal units. One class (CALCAREA) has calcareous (limestone) spicules that are sometimes quite elaborate; a second class (HEXACTINELLIDA) has spicules of glasslike silicon; a third class (DEMOSPONGIA) has either no skeleton at all, or a

skeleton composed of SPONGIN fibers, or a combination of spongin and silicious spicules.

The sponge of commerce is the cleaned and dried skeleton of certain species of Demospongia, having a pure spongin framework. Spongin is a soft, fibrous material capable in the dry state of absorbing much water. The principal sponge of commerce is *Euspongia*. A million or more pounds of sponge skeletons are marketed annually in the United States.

C. Reproduction

The sponge reproduces both sexually and asexually. Asexual reproduction is accomplished by two methods: *a*, ordinary budding, involving the branching off of a new individual from the external surface of an old one; and *b*, internal budding, or gemmulation, a process involving the aggregation of small bunches of cells of different sorts in the form of spherical GEMMULES, each of which is literally an infant sponge. The sexual method is much like that of the true Metazoa. Eggs and sperms are produced in the MESOGLŒA, or deeper tissue, of a single individual, for Grantia is HERMAPHRODITIC. Sperms come in contact with eggs and the latter are fertilized in typical fashion. Embryonic development takes place within the tissue of the parent and the young are later released by breaking out into the canals and being swept out with the current.

D. Commercial Value of Sponges

So important has the sponge industry grown, especially since the vast development of the automobile industry, that marine sponge farms have been established in which sponges are planted and harvested in the most systematic fashion. Live sponges of the best types (seed sponges) are cut up into very small cubes, each cube being wired to a cement disk, which is sunk to the bottom in those parts of the sea known to be favorable for sponge growth, such as, for example, along the Bahama coasts. In a few years these pieces grow to a size suitable for the market. This method not only increases the crop, but permits the individuals, through lack of crowding, to become more nearly perfect. This is but one instance of sea farming, a relatively undeveloped industry. In the future we shall do much more with the products of the sea than we have even dreamed of doing in the past.

E. Phylogenetic Relationships of the Sponges

There exist today no close relatives of the sponges. The closest affinities noted are with a group of Mastigophora (a phylum of Protozoa), known as Choanoflagellata, or collar-flagellates, and especially with the genus *Proterospongia*. These Protozoa are remarkably like the cells of sponges that line the excurrent canals. Sometimes the choanoflagellate Protozoa form small, but rather massive colonies with internal collarless cells that resemble the mesoglœa cells of sponges (see Fig. 108). Granted then that the sponges have been derived from a group of Protozoa that became extensively colonial and attained a certain degree of division of labor and organization, what relation might they have to other metazoan phyla? The belief today is that the sponges went up an evolutionary blind alley and have never given rise to any higher forms. The early adoption of sessile life and the failure to acquire well-defined axiate organization may have doomed them to a permanent lowly status. As we have already said, the sponge branch of the phylogenetic tree comes off near the bottom and is distinctly a side branch ending in many minor twigs, all of which are only sponges.

SUMMARY

1. The sponges are regarded as being so different from all other Metazoa that they are placed in a separate division of Metazoa, called Parazoa.
2. In sponges organization is loose, and a whole sponge has a type of structure more like a colony of Protozoa than like a typical metazoan.
3. A sponge has hundreds of mouths (incurrent pores), there is no definite digestive tract, no head, no nervous system. Individual cells engulf food particles and pass on nutriment to other cells. The external layer is a syncytium. Sponges reproduce asexually by budding and by means of gemmules. They also have a typical mode of sexual reproduction by means of eggs and sperms.
4. The different classes of sponges differ in their degree of complexity and in their different kinds of skeletal elements.
5. Sponges have considerable commercial value and are a product of sea farming.
6. Sponges are regarded as an early, unprogressive side line of evolution, ancestral to no higher groups, and probably derived from a group of Mastigophora, called Choanoflagellata.

CHAPTER XX

HYDRA

(PHYLUM CŒLENTERATA)

THE Phylum Cœlenterata is generally regarded as being the most primitive of the typical metazoan phyla. Cœlenterates, in contrast to the sponges (Parazoa), have an enteron, or digestive tract, and therefore introduce us to the upper division of Metazoa, the ENTEROZOA.

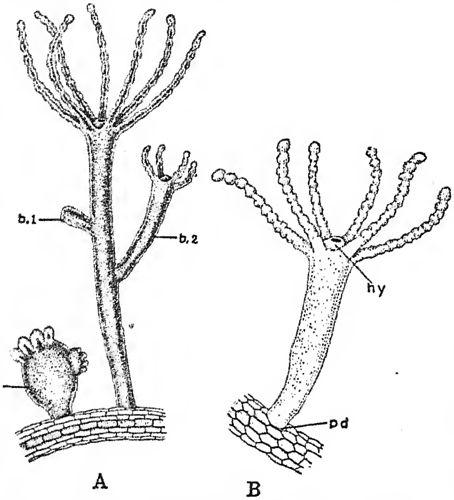


FIG. 114. Hydra attached to aquatic vegetation. A, two specimens of *Hydra viridissima*, the one on the right moderately extended; the one on the left in the fully contracted position (cp); b.1 and b.2 are, respectively, a young bud and an older bud. B, a specimen of *Hydra fusca;* hy, hypostome; pd, pedal disk. (Redrawn after Pfurtscheller wall chart.)

The fresh-water polyps, *Hydra* (*Chlorohydra*) *viridissima*, the green Hydra, and *Hydra* (*Pelmatohydra*) *oligactis*, the stalked Hydra, have long been favorite objects for laboratory study (Fig. 114). They are easily obtainable and, perhaps more important than anything else, they may be studied alive. Their feeding reactions and responses to changes in the environment are also readily observed. Hydra represents metazoan organization in almost its simplest terms. Relatives of Hydra (Protohydra and Microhydra) are considerably simpler than Hydra itself, and indeed rank as the very lowest expression of true metazoan organization.

Hydra lives in fresh water, usually attached by its "foot," or

basal extremity, to aquatic plants. It is not fixed in one position, though one might get this impression after watching it for a short time. It slides slowly about on its PEDAL DISK (pd) and in the course of some time it may travel considerable distances. We may characterize Hydra as a SEDENTARY organism in order to contrast it with SESSILE organisms that are permanently fixed.

A. Gross Anatomy

Plan of Organization.—Hydra is a true individual with a definite axiate organization. Roughly speaking, the body is an elongated cylinder. At the free end is the mouth and just back of the mouth a crown of tentacles radiating out from the mouth. The rest of the cylinder shows no differentiated organs except at the base, where there exists a pedal disk that functions as an adhesive and locomotor organ. A line drawn through the Hydra from the mouth and HYPOSTOME (Fig. 114, **B,** hy) to the pedal disk represents the primary axis of the animal. This is the oral-aboral axis and is not equivalent to the anteroposterior axis of higher animals, as will be made plain in a later chapter. The mouth and the ring of tentacles represent the apical or controlling region of the individual and the rest of the body is subordinate. It has been shown by ***Child*** and others that the rate of metabolism is greatest at the mouth end and that there is a gradient of lessening rate of chemical activity as one proceeds down the axis. The tips of the tentacles and the lips of the mouth are the most active regions of all and have the highest rates of metabolism. Most authors lose sight of the primary organization of Hydra in their efforts to emphasize the fact that the repeated parts are radially arranged. In the plan of organization this RADIAL SYMMETRY is secondary to the axis of polarity, which is essentially equivalent to what is called the ventrodorsal axis of higher forms; while the radial symmetry is comparable with the bilateral symmetry of these groups. All Metazoa have at least a primary axis. They vary with reference to their secondary plan of organization. Sessile and sedentary organisms are likely to be characterized by radial symmetry; while free-living organisms usually exhibit bilateral symmetry.

The Two-layered Structure of Hydra.—Another feature of the general plan of organization in Hydra is that it is DIPLOBLASTIC (Fig. 115, **A**)—by which is meant that the body consists of but two layers of cells, an ECTODERM (ec) layer on the outside and an EN-

DODERM (en) layer on the inside. The ectoderm is a protective, sensory, and contractile layer; while the endoderm is muscular and alimentary in character. One might compare the two-layered condition of Hydra to that of a thermos bottle, which consists of an outer and an inner cylinder, with the inner cylinder opening

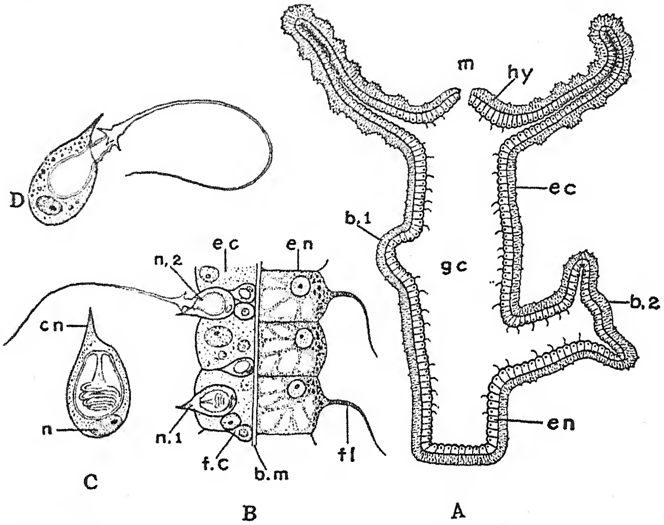


FIG. 115. Cellular structure of *Hydra*. A, a semidiagrammatic view emphasizing the diploblastic, or two-layered, condition: b.1 and b.2 are a younger and an older bud; ec, ectoderm; en, endoderm; gc, gastrovascular cavity; hy, hypostome; m, mouth. B, a semidiagrammatic section through the body wall of *Hydra*, showing: b.m, basement membrane or mesoglœa; ec, epithelio-muscular cell of the ectoderm; en, epithelio-muscular cell of the endoderm; fl, flagellum of latter cell; f.c, formative or subepithelial cells; n.1, nematocyst ready for discharge; n.2, nematocyst discharged. C, enlarged figure of a nematocyst before discharge; cn, cnidocil or trigger; n, nucleus of cnidoblast or cell in which nematocyst was formed. D, enlarged view of discharged nematocyst. (Redrawn after Pfurtscheller wall chart.)

at the mouth. In Hydra there is no open space between the two layers, but only a thin sheet of noncellular substance. The central cavity is known as the GASTROVASCULAR CAVITY (gc). It is the only cavity present in the body, for there is no cœlom nor any blood nor lymph spaces. This type of cavity differs from similar cavities of most higher organisms in having but one opening, the mouth, and no posterior opening, or anus. It also subserves two functions, that of digestion and that of circulating the products of digestion

about the body. It is therefore both a digestive tract and a vascular system; hence the name, "gastrovascular."

B. Histology of Hydra

We have already considered the main features of the general organization of Hydra and shall now turn our attention to the cellular composition of the animal. We have before us a true metazoan organism that makes use of cells to gain specialization of regions of the body. There is a physiological division of labor among the cells, some performing only one function, others performing two or three functions. In so far as more than one function is performed by one kind of cell, there is incomplete specialization. A study of the cellular details of the two layers of Hydra, the ectoderm and the endoderm, affords a good introduction to that important branch of morphology known as Histology. We may conveniently describe first those types of cells that are confined to the ectoderm; second, those confined to the endoderm; and third, those present in both ectoderm and endoderm.

1. *Cells Confined to the Ectoderm*

There may be distinguished three types of cells that are characteristically ectodermal: *a*, epithelio-muscular cells; *b*, nematocysts, or nettle cells; *c*, reproductive cells.

a. Epithelio-muscular Cells.—Hydra has no cells that are purely muscular in function, but each of the epithelial cells possesses

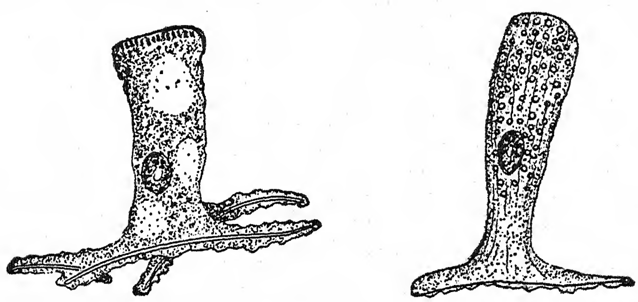


Fig. 116. Epithelio-muscular cells of *Hydra oligactis*, showing myofibrils and secretory granules. (From Schneider.)

elongated basal processes which extend up and down the cylinder of the body and contain contractile fibers (Fig. 116). The contraction of these muscular processes serves to shorten the body or to

bend it from side to side. The bodies of the epithelio-muscular cells lie side by side like paving blocks with free ends rounded. They serve the double function of covering the outer surface of the body and, by contraction, shortening the body when it is necessary to withdraw the oral end. In addition to this, ectoderm cells of the basal disk have the power of sending out pseudopodial processes by means of which the Hydra moves slowly from place to place.

b. Nettle Cells.—These cells are peculiar to the phylum Cœlenterata to which Hydra belongs. They occur over nearly the entire outer surface, being absent only on the basal disk. They are most abundant on the tentacles and on the HYPOSTOME, the crater-like prominence around the mouth. On the tentacles the stinging cells are usually arranged in batteries composed of one piece of heavy artillery (a large, specialized nematocyst) in the center and a ring of smaller fieldpieces about it. These curious cells serve as offensive or defensive weapons and are the only means a Hydra has of defending itself or of capturing prey. A nettle cell, or NEMATOCYST (Fig. 115, **B**, n.1 and n.2), as it is called when fully formed, is possessed of a coiled thread that lies inside of its body and that may be everted or shot out with great violence so as to penetrate the body of enemy or prey. From the end of the thread, a minute drop of poison exudes, which has a paralyzing effect upon animals struck by it. When many nettle cells strike at once, animals much larger than a Hydra may be paralyzed. Each nettle cell is provided with a sensory hair or CNIDOCIL (Fig. 115, **C**, cn), which plays the part of a trigger. When certain stimuli affect the trigger, it reacts in such a way as to bring about the discharge of the stinging thread.

A detailed study of the ***origin and development of nematocysts*** has shown that they are cytoplasmic derivatives of certain cells of the formative ectoderm. Within such a cell there arises a vesicular body, which in the course of development acquires a tough membrane. This vesicle or cyst increases in size until it crowds the nucleus to one side. While the cyst is growing, one part of its surface pouches inward and elongates into a slender coiled tube, the "thread" of the nematocyst (Fig. 115, **C**). This shoots out when the cell functions as a stinging cell (Fig. 115, **D**). The method of uncoiling is similar to that observed when the inturned finger of a glove is flipped out by blowing into the opening of the glove. The ***exact mechanism of this discharge*** is not fully understood, but

there is evidence that the force exerted in the discharge is due to an increase in the water content of the cyst. This increased internal pressure becomes focused upon the one part of the cyst that can yield, namely, the inturned threadlike tube, which everts with such incredible velocity that, even though it is slender and delicate, it is able to penetrate resistant tissues such as the skin of larger animals. In endeavoring to show how this is possible, certain writers call our attention to the alleged penetration of straws into tough wood when driven at high speed in a tornado.

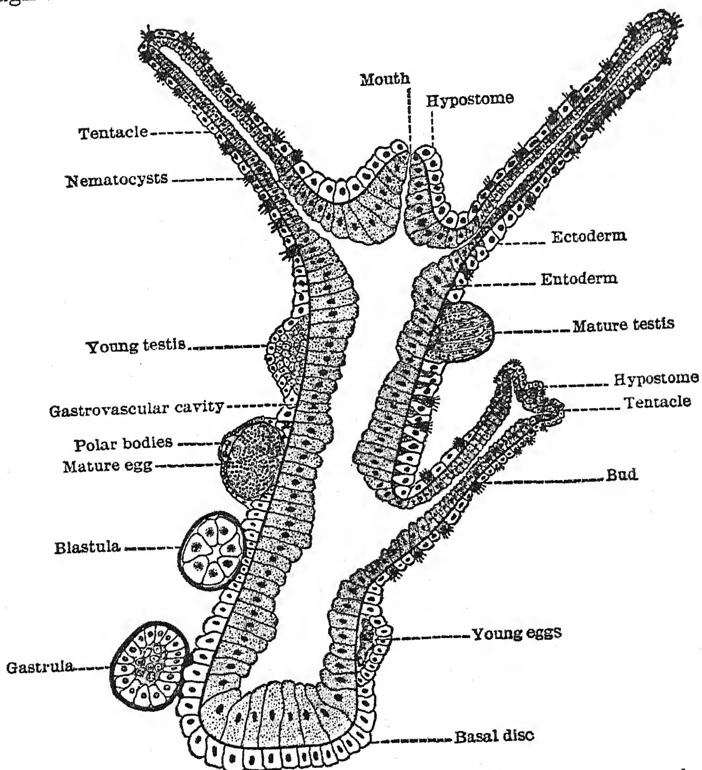


Fig. 117. A longitudinal section of *Hydra*. Not all the structures shown occur in one animal at the same time. (From Hegner.)

c. **Reproductive Cells.**—Like most sedentary and sessile organisms, Hydra may be MONŒCIOUS, or HERMAPHRODITIC; that is to say, each individual produces both male and female germ cells (Fig. 117). The germ cells are aggregated into more or less compact

masses, called GONADS. The male gonad is called a TESTIS and the female, an OVARY. In certain regions of the body and under certain environmental conditions, a group of undifferentiated formative cells begins to grow and to multiply, giving rise ultimately to one or other type of gonad. At first the two types of gonads and their contained primordial germ cells are indistinguishable, but later they become very different indeed. In the ovary there is a cannibalistic warfare among the primordial germ cells, the stronger engulfing and eating up the weaker until only one is left, a huge gorged cell filled with the remains of its sisters. In the testis the chief activity has been of another sort: the cells have gone on multiplying until there are immense numbers of minute very active sperms with swimming tails. In the case of ova, numbers have been sacrificed for the sake of a large accumulation of food for the prospective embryo; while in the case of the sperms, size and food have been sacrificed for great numbers and mobility.

2. *Cells Confined to the Endoderm*

There are three kinds of cells found only in the endoderm: *a*, nutritive-muscular cells; *b*, slime cells; *c*, albumen cells. These cells are all concerned with the processes of securing, digesting, and circulating the food.

a. Nutritive-muscular Cells.—These cells are larger and longer than the corresponding cells of the ectoderm; their free ends bear flagella (Fig. 115, **B**, en) and also send out pseudopodia that engulf food like those of Amœba. At their basal ends these cells have elongated muscular processes that run around the cylindrical body at right angles to the processes of the ectodermal muscular cells. Contraction of these muscles elongates the body, while contraction of the ectodermal muscles shortens it. The two sets of muscles together control all movements except the slow sliding movement of the basal disk. The cytoplasm of the endodermal nutritive-muscular cells is much vacuolated in well-fed Hydras and contains considerable food matter. In the green Hydra small green algæ live SYMBIOTICALLY inside alimentary cells. We see then that these cells are quite versatile, performing a variety of functions, each being almost able to take care of itself.

b. Slime Cells.—These cells are used to lubricate the food in order to facilitate swallowing. They are located between the epithelial cells of the mouth region.

c. Albumen Cells.—These are widely distributed elongated cells with slender bases attached to the basement membrane. Not infrequently the free ends of these cells are provided with one or more flagella.

3. *Cells Found in Both Ectoderm and Endoderm*

There are three kinds of cells not confined to either body layer, but distributed more or less at random throughout the body of Hydra: *a*, nerve cells; *b*, sensory cells; *c* formative or reserve cells.

a. Nerve Cells.—Specialized nerve cells are relatively few in Hydra. They are more abundant in the hypostome than elsewhere. In a sense then this region of the nervous system corre-

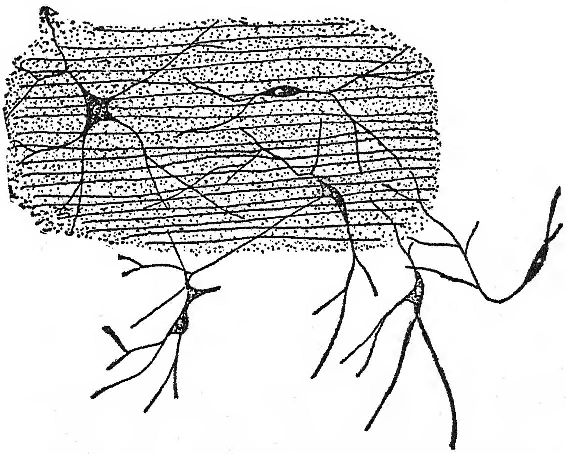


FIG. 118. Plexus of nerve cells in the ectoderm of *Hydra oligactis;* the parallel lines represent the longitudinal muscle fibers on the supporting lamella. (From Schneider.)

sponds to primitive brain, the center of its coördinated activities, by means of which the behavior of the organism as a whole is integrated or unified. There is no compact arrangement of the nerve cells into ganglia such as are found in the higher Metazoa, but the nerve cells are scattered and in contact only by means of their branching processes (Fig. 118). The nerve cells in the hypostome and all over the body are either united or are at least in contact by means of their processes, constituting what is known as a *nerve-net* type of nervous system. This arrangement makes for a sort of general response of the whole body whenever a suffi-

ciently strong stimulus is applied to any sensitive part of it. If a tentacle is strongly stimulated, not only does it contract but the other tentacles and the whole body contract. Such an arrangement might be likened to a telephone system so hooked up that when one bell rings, all the bells connected with the exchange ring at the same time—not a very efficient system, to be sure.

b. Sensory Cells.—Cells specialized for receiving stimuli are found chiefly around the mouth and the basal disk. These are slender cells, lying crowded between the epithelial cells and sending out from their bases branching fibers connecting them with the muscular processes of the contractile cells and with the nerve cells. Sensory cells are much more numerous in the endoderm than in the ectoderm; in addition, those of the endoderm sometimes bear flagella.

c. Formative or Reserve Cells.—There are always present, in the corners made by the tapering basal ends of the epithelial cells, little groups of roundish cells that are not specialized for any particular function, but are always ready for any one of several various lines of specialization (Fig. 115, **B**, f.c). Those in the ectoderm differentiate into epithelio-muscular cells, nettle cells, germ cells, and probably also into nerve and sensory cells. Those in the endoderm seem to specialize into various types of endodermal tissues only when repair work is necessary as the result of injury, or when a bud is being formed. Formative cells are far more abundant in the ectoderm than in the endoderm.

4. *The Basement Membrane, or Mesoglœa*

A thin homogeneous layer, secreted mutually by the ectoderm and the endoderm, lies between the two body layers (Fig. 115, **B**, b.m). In Hydra and in the other polypoid types of Cœlenterata the mesoglœa remains relatively inconspicuous, assuming the form of a thin basement membrane, but in the jellyfish types it becomes a voluminous mass of jelly containing scattered cells and constitutes the main bulk of the body.

C. Physiology of Hydra

1. *How Hydra Feeds*

Hydra is a carnivorous animal, voracious and greedy beyond compare. It feeds upon whatever forms of animals it may be able

to reach and to sting with its batteries of nettle cells. Usually it has to be satisfied with the capture of small crustaceans or larvæ of aquatic animals. ***Jennings,*** however, has described a case that breaks all records for greed. A Hydra was found that had swallowed a caterpillar about fifty times its own size. The Hydra's body was stretched like a thin film over the body of its prey, and the mouth and tentacles formed the only clearly visible evidence that the Hydra was on the outside of the caterpillar. Whether the meal was ever digested is not known, but it seems certain that there must have ensued a severe attack of indigestion. Hydras are rarely so greedy as this, their favorite food consisting of creatures of more convenient size, such as the water flea, Daphnia. One of these water fleas in swimming about comes into contact with a stretched out tentacle of Hydra and is at once stung by the poisoned darts of the nettle cells. The poisonous material, HYPNOTOXIN, paralyzes the prey, while the threads hold it firmly. With the aid of other tentacles it is passed to the mouth, which opens in anticipation, indicating a nervous connection between the tentacles and the mouth. The Daphnia is then forced into the gastrovascular cavity, where it is digested, just as a piece of meat would be digested in a human digestive tract, by means of a pouring forth into the cavity of digestive ferments. Indigestible parts of the animal are voided through the mouth. Small organisms or other minute food particles are commonly engulfed by the pseudopodial action of the endodermal cells and are digested within the bodies of the cells. Thus Hydra exhibits two modes of digestion, the primitive method of engulfing and digesting food within single cells (INTRACELLULAR DIGESTION) and the more advanced method of making use of a digestive cavity surrounded by a layer of cells (EXTRACELLULAR DIGESTION).

2. *The Behavior of Hydra*

The green fresh-water polyp (*Hydra viridissima*) is a good deal livelier than other species and is therefore a better form for the study of behavior. The more sluggish forms have much the same activities, but in a slowed down form. Hydras are usually found attached to the glass bottoms or sides of aquaria, clinging to water plants or hanging head downward from the surface film of the water. They tend to take up a position perpendicular to the surface of attachment. Movements of Hydra while attached to the

substratum are confined to those produced by contraction of the muscular processes of the two kinds of epithelial cells. All they can do is to contract by shortening the muscular processes of the ectodermal cells or to elongate through contraction of endodermal muscular processes. Movements may be stimulated by internal conditions, such as hunger, or by external stimuli.

3. *Hunger Movements*

A hungry Hydra goes through a regular routine of activities. It contracts the endodermal cells and in so doing extends the body as far as possible, spreading out the tentacles to all points of the compass. If no food is encountered, it contracts and then extends in a different direction. If this new direction brings no success,

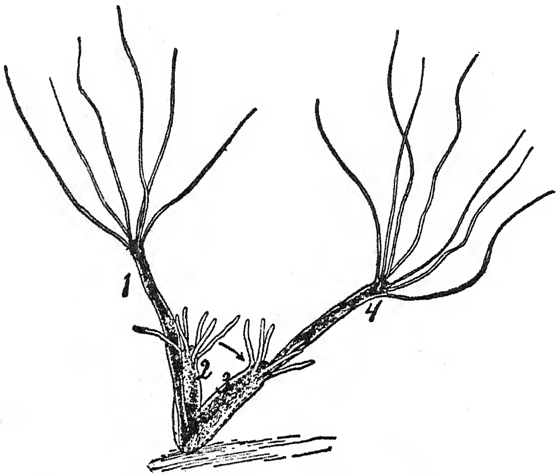


FIG. 119. Spontaneous changes of positions in an undisturbed *Hydra*. Side view. The extended animal (*1*), contracts (*2*), bends to a new position (*3*), and then extends (*4*). (From Jennings.)

it will suddenly contract again and try still another direction (Fig. 119). This is the equivalent of the TRIAL-AND-ERROR MOVEMENTS of Paramecium. If the now very hungry Hydra can find no food after repeated trials, it adopts another type of behavior involving a change of headquarters. At first it will simply slide along on its basal disk until it has gone a short distance; it then goes through trial-and-error movements again. If still unsuccessful, it adopts more strenuous measures, bending over sideways toward the plane

of attachment, attaching itself by the tentacles, releasing the basal disk, contracting the body, and then taking an upright position in a new place. This may be repeated much after the fashion of a measuring worm looping along a twig (Fig. 120). If no food be encountered—and none is likely to be under the conditions of the experiment—the ravenous Hydra resorts to extreme measures, somersaulting instead of looping. This is its last resort in the attainment of speed. The head is bent over and attached; then the foot is thrown forward over the head and attached again far in advance; then the head does as the foot had done. Even this gives no satisfaction, and the Hydra finally contracts down to a lemon-shaped mass and becomes very quiet, as though discouraged. It will live for a long time in the contracted, quiescent condition. All of this behavior seems to indicate that Hydra is intelligent; and doubtless it really is intelligent, if we are somewhat liberal in our definition of the term. If ability to modify behavior according to the changing conditions of life is intelligence, Hydra is intelligent.

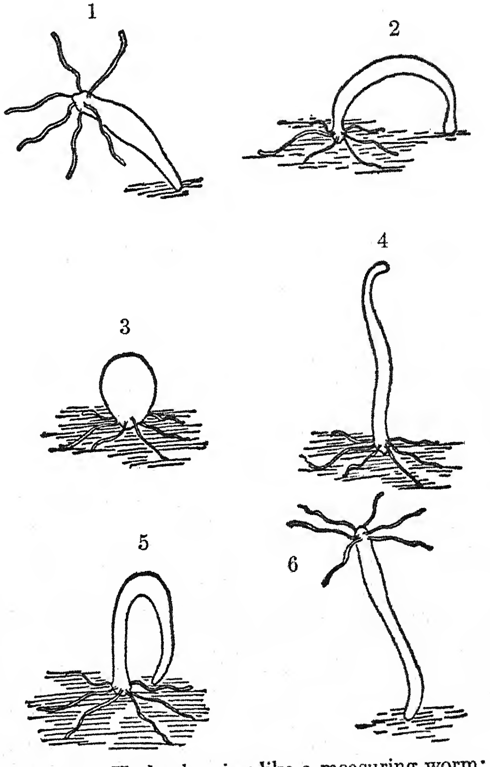


FIG. 120. Hydra looping like a measuring worm; 1–6 show successive positions of a single individual. (From Jennings, after Wagner.)

4. *Reactions to External Stimuli*

A good many different kinds of stimuli affect the behavior of Hydra, the following being its most important reactions: reac-

tions to contact, reactions to chemicals, reactions to light, reactions to temperature changes.

a. **Thigmotropism** (reactions to contacts).—Because Hydra is a sedentary organism, fixed at all times to a substratum, contact stimuli are of primary significance. The normal position of Hydra with the foot attached, and both looping and somersaulting movements, have definite reference to contacts. Hydras are also very sensitive to mechanical shocks such as jarring of the vessel in which they are contained, or to being touched with a solid object such as a glass rod. If one tentacle be touched, others contract, showing transmission of stimuli through the network of nerve cells and out to other tentacles. If one side of the body be touched, it contracts on that side and bends away at the point of local stimulus.

b. **Chemotropism.**—Hydra does not discharge its nematocysts when mere mechanical stimulation is applied unless the mechanical shock be severe or oft repeated. To cause the discharge a definite combination of both chemical and mechanical stimuli is necessary. This combination is furnished when solid protein food is brought in contact with the tentacles.

c. **Phototropism.**—One may easily observe that, if the aquarium be placed in such a position that the different sides have different illumination, the Hydras are likely to be found on one or possibly two sides, depending on the intensity of the light. Green Hydras tend to gather on the lighter sides of the aquarium unless there is too much direct sunlight. The method by which they reach the area of optimum light is that of trial-and-error; that is, continual avoidance of the less favorable of two alternatives will inevitably result in reaching the most favorable region and in remaining there.

d. **Thermotropism.**—If Hydras are placed in a long aquarium warmed at one end and chilled at the other, they will find by trial-and-error the region of optimum temperature, and stay there. If the whole environment be warmed, the Hydras become at first more active; but no migratory movements take place unless the temperature goes above 31° C. If the temperature be lowered, Hydra merely becomes less active, finally ceasing all movement when the freezing point is approached. When exposed to temperatures that are too high or too low the animals contract to as great an extent as possible and remain quiescent until favorable conditions return, or until they die.

D. Reproduction of Hydra

Two phases are to be distinguished in the life cycle of Hydra and these are comparable to those described for Paramecium. There is an ASEXUAL method of reproduction, much like binary fission, which is called budding; and there is a SEXUAL method involving the production of male and female gametes—eggs and spermatozoa—and the union of gametes, or fertilization.

1. *Budding*

Hydras reproducing by budding are not uncommon in aquaria kept in laboratories (Fig. 114, **A**, 115, **A**, and 117). The first sign of budding is seen in a slight bump on the side of the body (Fig. 115, **A**, b.1), usually midway between the mouth and the basal disk. This bump grows out at right angles to the parent body as a cylindrical branch (Fig. 114, **A**, b.1), and soon develops a crown of tentacles and a mouth at the free end (Fig. 114, **A**, b.2). While growing, the gastrovascular cavity of the bud remains in communication with that of the parent; but, when full grown, the budded individual pinches off and becomes independent. Not infrequently two or more buds may be seen attached to the parent body at the same time, so that there exists, for a while at least, a simple colony of polyps. Budding takes place only in well-fed, large Hydras. If a budding individual be starved, the bud ceases to grow and will be resorbed by the starving parent.

2. *Sexual Reproduction*

In our account of the histology of Hydra we have already shown that both male and female sex cells, or gametes, arise through the differentiation of formative or undifferentiated cells of the ectoderm. While these primordial germ cells are at first alike, the history of differentiation of the male cells is quite different from that of the female. The two histories are now to be described separately. This history of the differentiation and maturation of spermatozoa is known as SPERMATOGENESIS; that of ova, or eggs, as OÖGENESIS.

a. Spermatogenesis.—The male gametes are formed in small conical enlargements, which project from the surface of the body. These enlargements are the male gonads, TESTES, or SPERMARIES (Fig. 117). The testes are the result of regional rapid mitotic divi-

sion of a group of formative cells in the ectoderm. These cells come to arrange themselves into a number of vertically placed elongated sacs or cysts (Fig. 121), each of which is a continuous mass of cytoplasm containing many nuclei. After the period of multiplication of nuclei is over each nucleus contains the diploid, or somatic, number of chromosomes and is known as a SPERMATOGONIUM. Soon after this the chromosomes unite in pairs, giving half as many double chromosomes as there had previously been single chromosomes. The cells are now full grown and are known as PRIMARY SPERMATOCYTES. These then divide, one member of each of the double chromosomes going to each daughter cell. This is the first maturation division and is a REDUCTION DIVISION, for the number of chromosomes in each cell has been reduced to one half. These reduced cells are called SECONDARY SPERMATOCYTES. They divide again, without reducing the chromosome number, into SPERMATIDS, which in turn gradually differentiate into the tailed SPERMATOZOA. Any one cyst may contain all the stages of male germ cells from the spermatogonia up to spermatozoa, the former occupying the inner end and the latter the outer end of the cyst. When a considerable number of ripe spermatozoa is formed, the testis ruptures and releases them into the water where they are able to swim about rapidly, and thus to reach the egg.

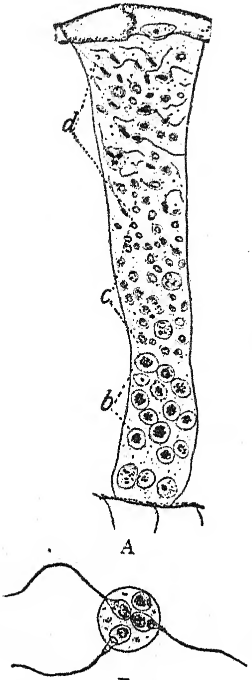


FIG. 121. Parts of a testis of *Hydra*. A, a single cyst showing spermatogonia, primary spermatocytes (*b*), secondary spermatocytes and spermatids (*c*), and spermatozoa (*d*); B, developing spermatozoa. (After Tannreuther in Biol. Bul.)

b. Oögenesis.—The female gonads, ovaries (Fig. 117), arise nearer the basal disk than do the testes. The formative cells destined to become the female germ cells divide less rapidly than do those in the testis, and on that account grow larger in size. They are first to be distinguished from ordinary formative cells by their larger, rounder form and by their larger nuclei. A consider-

able number of primordial egg cells constitutes the female gonad, or ovary; yet all but one of these potential egg cells are sacrificed for the purpose of enriching one of them. The one egg engulfs all of the other potential eggs and uses their substance as a kind of yolk (Fig. 122, A). Finally, the egg, which during the growing and feeding period has been amœboid in shape, rounds up into a sphere, surrounded by a single somewhat stretched layer of epithelial cells (Fig. 117). Maturation ensues, consisting, as in spermatogen-

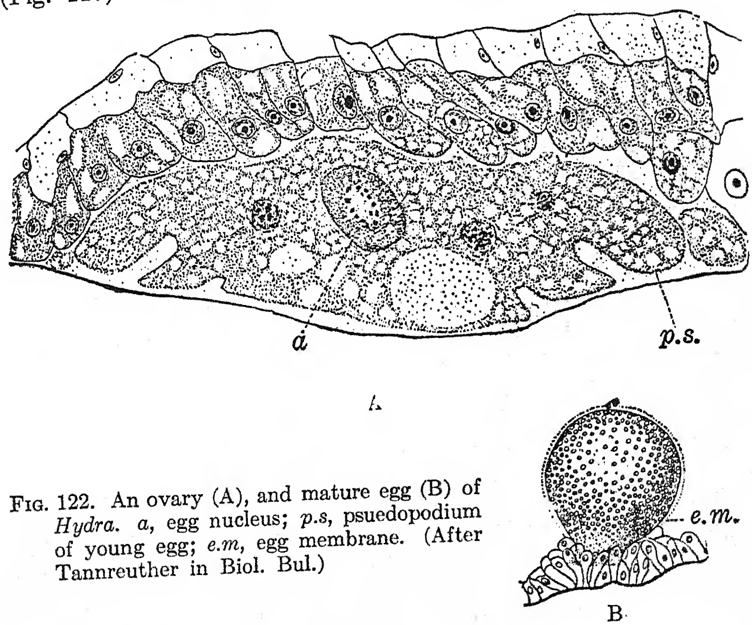


Fig. 122. An ovary (A), and mature egg (B) of *Hydra*. *a*, egg nucleus; *p.s*, psuedopodium of young egg; *e.m*, egg membrane. (After Tannreuther in Biol. Bul.)

esis, of two divisions; but here the divisions are very unequal in so far as the cytoplasm is concerned. Two very tiny cells, the POLAR BODIES, really abortive eggs, are formed (Fig. 122, B). During maturation the number of chromosomes, in the same manner as in spermatogenesis, is decreased to half of the original number. After maturation the ectodermal covering of the egg ruptures and the naked egg is exposed except at its base.

c. **Fertilization.**—The exposed egg seems to attract any spermatozoa that may be in the neighborhood. These swim to the egg in considerable numbers and several attach themselves to its surface. Only one, however, actually enters the egg. After the

sperm is inside of the egg membrane it rounds up into a nucleus and the egg and sperm nuclei unite to form a fusion nucleus in which the full specific number of chromosomes is reinstated. Unless it be fertilized the egg dies and disintegrates within a period of about twenty-four hours.

3. *Embryology*

After the egg is fertilized the development of a new individual begins. While still attached to the parent body it undergoes cleavage by mitotic division into cells known as BLASTOMERES. Cleavage continues until a hollow ball of cells, the BLASTULA (Fig. 117) is formed. This consists of a single layer of cells inclosing a SEGMENTATION CAVITY. Cells from the outer layer then begin to migrate into the cavity and ultimately fill it up. The inner cells are destined to form the endoderm, and hence the process of GASTRULATION, though not at all typical, has taken place; for, irrespective of just how the condition be arrived at, the attainment of the two-layered condition is considered as gastrulation (Fig. 117). While gastrulation has been going on, the ectoderm secretes about itself a horny layer, which acts as a protective envelope and effectually slows down and practically stops development for a considerable period. The young embryo drops to the bottom and rests for some time, usually passing the winter months in the dormant state. When environmental conditions again become favorable, the shell about the embryo is ruptured and the embryo is freed. The whole body undergoes expansion; the endoderm, hitherto solid, opens up so as to form the gastrovascular cavity; the mouth breaks through; the tentacles develop; and a young Hydra with its foot attached to the substratum starts out on its lifelong hunt for food.

4. *Regeneration*

An artificial method of reproducing Hydras is that of cutting a single individual into two or more parts and letting each part reproduce the whole. Regeneration is the process of reconstituting a whole individual or a whole organ from a part. It is a process characteristic of lowly organisms in which there is not too much regional specialization, or of young organisms that have not yet become specialized. A piece of Hydra as small as one twenty-fourth of the whole is capable of regenerating an entire animal.

E. The Relatives of Hydra

The Phylum Cœlenterata, to which Hydra belongs, is a very large and highly diversified group of animals, consisting of polyps, jellyfishes, corals, sea anemones, etc. They all agree in having

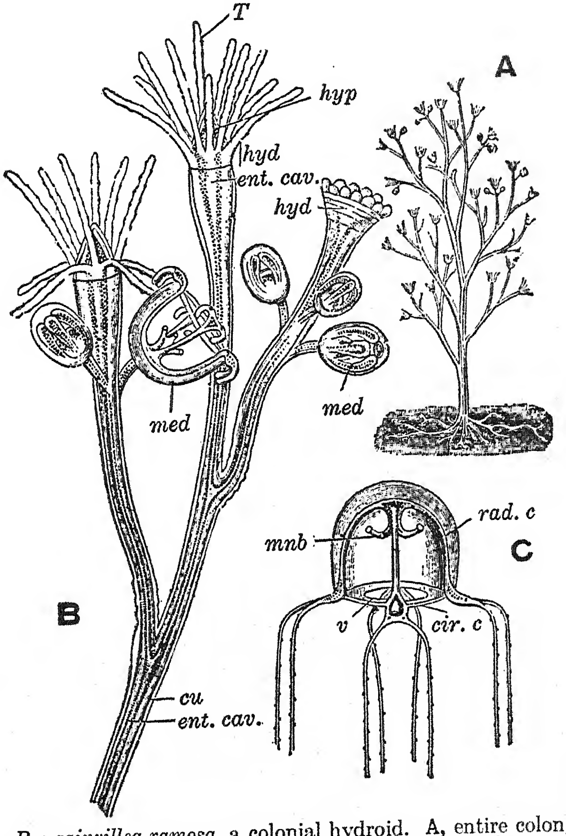


Fig. 123. *Bougainvillea ramosa*, a colonial hydroid. A, entire colony, natural size; B, portion of the same, magnified; C, immature medusa; *cir. c*, circular canal; *cu*, cuticle, or perisarc; *ent. cav.*, enteric, or gastrovascular cavity; *hyd*, polyp, or hydranth; *hyp*, hypostome, or manubrium; *med*, medusa bud; *mnb*, manubrium; *rad. c*, radial canal; *T*, tentacle; *v*, velum. (From Parker and Haswell, after Parker.)

but two body layers (diploblastic); in having no cœlom, or cavity between body wall and alimentary tract; in having a gastrovascular cavity with one opening, the mouth; and in possessing nematocysts.

There are three classes of Cœlenterata:—

Class I. Hydrozoa—including fresh-water polyps, colonial hydroids, some small jellyfishes, and a few coral-like forms.

Class II. Scyphozoa—including most of the larger jellyfishes.

Class III. Anthozoa—including the sea anemones and most of the corals.

Hydra is probably a degenerate type of the Class Hydrozoa and is therefore hardly representative of that class. Most of the Hydrozoa are colonial in the polyp phase of their life cycle and form rather elaborate branching systems of polyps derived from the budding of one young polyp. A good example of the Hydrozoa is Bougainvillea (Fig. 123), in which each individual polyp is the equivalent of a Hydra bud that has failed to detach itself from the parent body. Certain colonial Hydrozoa (Siphonophora) have some of their polyps specialized for locomotion, others for floats, others for defense (see Fig. 20). In fact, it is rather general for the members of a colony to differ somewhat in function. Bougainvillea shows a differentiation into generalized vegetative polyps (Fig. 123) and reproductive polyps or MEDUSÆ, which are characteristically umbrella-shaped and swim about freely in the sea. The medusa is a sexually mature individual that produces either eggs or sperms. The egg becomes fertilized and develops into a polyp, which in turn, by repeated asexual budding, forms a colony. Thus we have an alternation between the asexual and the sexual modes of reproduction quite similar to that seen in Paramecium. This is called METAGENESIS, or ALTERNATION OF GENERATIONS. Hydra is a degenerate form which has no true medusa stage, though the ovaries and testes may be viewed as reduced medusa buds. There are many intermediate conditions that serve to bridge the gap between species like Bougainvillea and Hydra.

In the Scyphozoa the medusa stage is highly developed and the polyp stage greatly reduced or suppressed; while in the Anthozoa the polyp stage is highly specialized and the medusa stage totally suppressed.

SUMMARY

1. The various species of Hydra studied in laboratories belong to the Subkingdom Metazoa, the Phylum Cœlenterata, and the Class Hydrozoa, a group characterized by being mostly colonial and having both the hydroid and medusa stage of metagenesis clearly defined, but with chief emphasis on the hydroid stage.

2. Hydra exhibits a well-defined axiate organization, with a primary axis running from oral to aboral ends, and typical radial symmetry at all levels of the primary axis.

3. Like all cœlenterates, Hydra is diploblastic; the internal cavity is a gastrovascular cavity performing the double function of digestion and circulation; both ectoderm and endoderm are differentiated into a number of specialized tissues; this differentiation of somatic tissues well illustrates the chief advance made by Metazoa over Protozoa; nematocysts are special intracellular mechanisms of offense and defense especially characteristic of cœlenterates; the nervous system has a nerve-net construction; between ectoderm and endoderm is a gelatinous layer, sometimes containing scattered cells, which is called the mesoglœa and is not true mesoderm.

4. Hydra is a degenerate representative of the Hydrozoa in which the medusa stage of metagenesis is omitted.

5. Hydra is carnivorous, swallowing water fleas and other animals, which it partly digests extracellularly by means of enzymes secreted into the gastrovascular cavity by gland cells, but some endoderm cells engulf food particles amœba-fashion and hence exhibit intracellular digestion.

6. The behavior of Hydra is complex and can hardly be summarized; sufficient to say that it exhibits the various kinds of tropisms characteristic of Protozoa, as well as the trial-and-error mode of reaction.

7. Reproduction of Hydra is both asexual (budding) and sexual. These two methods are telescoped into one generation instead of being separated the one into the hydroid generation and the other into the medusoid generation as is the case with typical Hydrozoa.

8. The modes of gamete formation and fertilization in Hydra are essentially equivalent to those found in the highest animals.

9. The egg, after fertilization, undergoes cleavage, forms a blastula and a gastrula stage, and then undergoes its further differentiation at a gastrula level.

10. Hydra exhibits extraordinary powers of regeneration of a whole individual from a severed part of the body. It has been a favored type for regeneration experiments.

11. The other classes of Cœlenterata (colonial Hydrozoa, Scyphozoa, and Anthozoa) are compared, with chief emphasis on the various modifications of metagenesis exhibited by them.

12. The Cœlenterata are regarded as the ancestral group from which all higher Metazoa have descended, but none of the existing cœlenterates should be considered as ancestral to any contemporaneous group.

CHAPTER XXI

PLANARIA

(PHYLUM PLATYHELMINTHES)

A. Habits and Habitat

Planaria is a common flatworm belonging to the Phylum Platyhelminthes. It occurs only in fresh water, usually crawling on the under sides of stones or other smooth objects. The body is several times as long as it is broad. It always moves about with the blunt anterior end foremost. The head end is rather broad with two lateral earlike processes, the auricles, which act as tactile organs. The posterior end tapers off to a sharp point. A well-grown animal may be half an inch long by about an eighth of an inch wide. When viewed from the side, the body is seen to

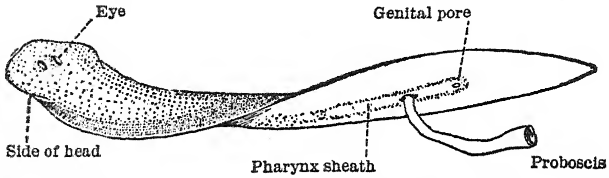


Fig. 124. *Planaria polychroa* seen in approximately side view, showing the flatness of the body and the way in which the proboscis may be thrust out. (From Shipley and MacBride.)

be extremely flat, a character which gives the common name flatworms to the group (Fig. 124). While a Hydra is in contact with solid objects only at its base, Planaria maintains contact along its entire length, about half of its body surface being kept constantly flat against the substratum.

Planaria has a very steady, gliding type of locomotion that seems to have no reference to any muscular movements of the body. Its progression is, in fact, due to cilia, which cover the entire surface but are particularly abundant on the ventral side. The worm lays down a smooth roadbed for itself by secreting mucus at the anterior end and then sliding along on it by backward whipping of the cilia. As it glides along, the head moves

from side to side and the auricles extend outward and forward, now to one side, now to the other, as though the animal were feeling its way.

B. General Morphology

1. *Four Advanced Characters of Planaria*

One can readily note that there are present in Planaria four characters not shown in Cœlenterata, but possessed also by higher groups: *a*, anteroposterior axis, ventrodorsal axis, and bilateral symmetry; *b*, a distinct third body layer, the mesoderm; *c*, an excretory system; *d*, a true central nervous system. These require detailed description:—

a. Anteroposterior Axis, Ventrodorsal Axis, and Bilateral Symmetry.—A modern theory as to the relation between the oral-aboral axis and radial symmetry of the cœlenterates, on the one hand, and the anteroposterior axis, ventrodorsal axis, and bilateral symmetry of the flatworms, on the other, deserves careful consideration.

This theory holds that the flatworms have descended from some flat-bodied, jellyfish-like ancestor. Such a form would have had its mouth at the free end of a long hypostome resembling a handle hanging down from the top of the flat umbrella-like body. The pharynx of such a form would divide into a number of branching radial subdivisions of the gastrovascular cavity. The central nervous system would consist of radially arranged ganglia, repeated at regular intervals along the margin of the umbrella and connected with one another by nerve cords, the whole forming a nerve ring.

If in the course of evolution such a jellyfish were to lose the habit of swimming about freely in the water, as many other types of aquatic organisms seem to have done, and were to settle to the bottom for feeding purposes, it would settle down on the oral surface with the mouth next to the bottom. In feeding upon the rich food supply of the bottom it would tend to slide about on the oral surface by muscular and ciliary action, and it would progress sometimes in the direction of one radial axis, sometimes in others. For some unknown reason one of the several radial axes seems to have gained the ascendancy, becoming the new apical end, or head, and the ganglia of that region became the new brain. The

acquisition of dominance by the new brain seems to have suppressed all rival nerve centers, and all that is left of the ancestral ganglionic ring are one enlarged pair of ganglia and a pair of widely separated nerve cords.

The establishment of a new dominant region, the head, would influence the direction of growth of the rest of the body, involving an elongation perpendicularly to the apical region, and oval or elongated bodies would be produced. The mouth would still be centrally located and the hypostome would now be used as a proboscis. The digestive tract would still be a more or less radially branched gastrovascular system with the branches coming off from the pharynx and running to all parts of the body, but mainly forward and backward because of the elongation of body.

In short, were these changes to take place, a primitive flatworm would be the result. There are numerous flatworms today, relatives of Planaria, that are so wide across the body as to be broadly oval or nearly circular in shape. A comparison of these with a flat jellyfish lends probability to the above theory.

According to this theory the oral-aboral axis of the cœlenterates becomes the ventrodorsal axis of flatworms and the radial symmetry of cœlenterates becomes not merely the bilateral symmetry but the anteroposterior axis of the flatworms, for one of the secondary radial apical points of the circular marginal nervous system of the jellyfish ancestor becomes the new anterior end, head, of the flatworm. Hence it is not the ventrodorsal axis that is new, as is usually supposed to be the case, but the anteroposterior axis, while bilateral symmetry is merely a kind of distortion of radial symmetry consequent upon the elongation of the body perpendicular to the new apical end. Although it must be admitted that this theory is somewhat speculative, it is undoubtedly the most satisfactory theory of the ancestry of the flatworms and is in harmony with the Diphyletic Tree Theory.

In all animals except vertebrates the ventral surface is the one where lies the nervous system; it is the superior or controlling surface, and there is a gradient in the rate of metabolic activity running from ventral to dorsal surfaces. One might call such a gradient a ventrodorsal gradient to distinguish it from the dorsoventral gradient of vertebrates. An animal with a ventrodorsal axis is related to the environment equally on the two sides, the right and the left; and in accord with this we find that the two

sides are equivalents or mirror images of each other. One can draw a line down the body from head to tail so as to divide the animal into two equivalent halves. Some organs occur singly in the median line, such as mouth and proboscis, penis, uterus, genital pore, and the median branch of the intestine; but all organs that occur away from the median line are likely to be paired. Thus we have a pair of brains, a pair of eyes, a pair of auricles, a pair of posterior gastrovascular branches, and pairs of gonads. This paired arrangement is known as BILATERAL SYMMETRY. All of the higher animals are, at least primitively, bilaterally symmetrical.

b. The Mesoderm.—Hydra is diploblastic, having only two body layers, ectoderm and endoderm, with a noncellular mesoglœa between. Planaria, however, is a three-layered animal (TRIPLOBLASTIC), as are all higher animals. In addition to the ectoderm and endoderm there is a third body layer known as mesoderm.

The ECTODERM consists of a thin layer of external cells called the EPIDERMIS. The cells are ciliated. Imbedded in the epidermis are characteristic rodlike bodies, called RHABDITES, which are discharged to the exterior when the animal is irritated, and are believed to serve an offensive purpose. The skin is also provided with unicellular mucous glands.

The MESODERM consists largely of a sort of packing tissue, or PARENCHYMA, which rather loosely fills in the space unoccupied by other organs between the body wall and the alimentary tract. Thus there is no definite cœlom, or body cavity. Because the mesoderm is not organized to form a definite epithelium lining the body cavity, it is considered by some zoölogists as not true mesoderm but mesenchyme. Other mesodermal tissues are the muscles which occur in four systems: circular muscles, longitudinal muscles, oblique, and dorsoventral muscles. The circular muscle cells form a thin layer next to the epidermis; then comes an ill-defined layer of longitudinal and oblique muscles; the dorsoventral muscles extend between dorsal and ventral surfaces between the branches of the intestine.

The ENDODERM consists of a single layer of elongated epithelial cells lining the much-branched gastrovascular cavity.

c. Excretory System.—This consists of a network of tubules running lengthwise through the body along the two sides. Each tube branches and rebranches giving off fine terminal twigs to all parts of the body. Each ultimate branch terminates in a peculiar

cell termed a FLAME CELL (Fig. 125), a large hollow cell in the cavity of which there is a bunch of cilia. These cilia extend into the cavity of the tubule and their synchronous beat produces a flicker like that of a flame. Their movement serves to propel the fluid contents of the tubule and thus to drive it into the excretory ducts which open to the exterior.

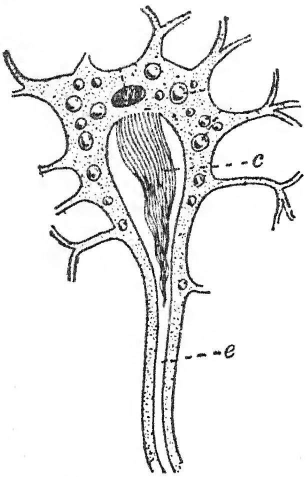


FIG. 125. Flame cell of *Planaria*. *c*, cilia; *e*, opening into excretory tubule. (From Lankester's Treatise.)

d. Nervous System.—The central nervous system consists of a bilobed mass of nerve cells (CEPHALIC GANGLIA) near the anterior end and beneath the black EYE-SPOTS. This double ganglion, or BRAIN, gives off two ventral nerve cords that run the length of the body at some distance from each other. Transverse nerves connect the two ventral nerve cords like the rungs of a ladder. The brain also gives off nerves to the various sensitive areas of the head, the AURICLES, and adjacent surfaces.

2. *Improvements on Earlier Systems*

The systems showing most distinct improvement over equivalent systems of Hydra are: the alimentary system, the reproductive system, and the muscular system.

a. Alimentary System.—About midway between anterior and posterior ends of Planaria is the pharyngeal chamber in which lies a cylindrical muscular tube, the PHARYNX (Fig. 126). This organ is continuous anteriorly with the walls of the PHARYNGEAL CHAMBER and with the GASTROVASCULAR CAVITY. It is free at the posterior end and has a wide terminal opening near the MOUTH. The pharyngeal chamber opens to the exterior through a circular opening, and, when feeding, the pharynx may be protruded by elongation through this opening, as a long trunk or PROBOSCIS (Fig. 124). The digestive tract is a true GASTROVASCULAR CAVITY, like that of Hydra, but much more elaborately branched, so as to be in close contact with nearly every part of the body. It is thus able not

only to digest food but also possibly to circulate it. There is only one opening into this cavity, namely, the mouth, no anus being present. Fæces are voided through the mouth, as in Hydra.

b. Reproductive System.—Planaria, like most flatworms that reproduce sexually, is HERMAPHRODITIC, i.e., it has both male and female reproductive organs in the same individual (Fig. 126). Some Hydras were shown to be hermaphrodites also; so this is not a new but an old character. As a rule, the hermaphrodite condition is found in groups that have sedentary habits, or are likely to lead isolated lives. It makes the process of fertilization of eggs more certain when a single individual can fertilize its own eggs, or when any two individuals that chance to meet can mutually supply sperm for each other's eggs.

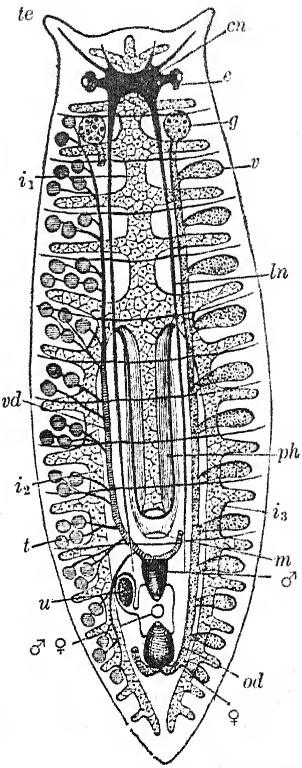


FIG. 126. Anatomy of *Planaria*. *cn*, brain; *e*, eye; *g*, ovary; i_1, i_2, i_3, branches of intestine; *ln*, lateral nerve; *m*, mouth; *ph*, pharynx; *od*, oviduct; *t*, testis; *te*, auricle; *u*, uterus; *v*, yolk glands; *vd*, vas deferens; ♂, penis; ♀, vagina; ♂ ♀, common genital pore. (From Lankester's Treatise, after V. Graff.)

The MALE REPRODUCTIVE ORGANS consist of a large number of small spherical bodies (TESTES) located in the mesoderm and scattered almost from one end of the body to the other. They are connected by tubules with a pair of ducts, the VASA DEFERENTIA, that lead to a median muscular organ, the PENIS, which lies in a pouch of the body wall called the PENIAL SHEATH; this opens to the outside by means of a single opening, the GENITAL PORE. When the free end of the penis is protruded, it is of considerable length and is able to pass into the long slender duct of the uterus of another individual to which it transfers spermatophores or packets of spermatozoa.

The FEMALE REPRODUCTIVE ORGANS consist of two spherical OVARIES lying near the anterior end. Each is provided with a long oviduct which runs backward to the posterior end of the body and enters the genital atrium. As the eggs pass down the oviduct they become associated with yolk from the numerous yolk glands that empty into the oviduct. Thus eggs mixed with yolk enter the genital atrium where sperm cells have been stored, and there fertilization takes place. After the eggs are fertilized groups of them together with masses of yolk are parceled up into cocoons. These capsule-like bodies are commonly deposited upon stones or other objects in water where they remain until the young worms emerge. One cannot but be impressed with the elaborateness of the whole equipment for sexual reproduction. It is, indeed, a well-known fact that flatworms, more than almost any other group of animals, have developed a high degree of specialization in the organs accessory to sexual reproduction.

c. Muscular System.—In the Hydra we saw that the contractile function was played by cells that had also a number of other duties. In Planaria there are cells that are specialized for the contractile or muscular function alone.

3. *Systems That Planaria Lacks*

A number of important systems that are prominent features of higher animals are not definitely differentiated in Planaria nor in other flatworms: (1) There is no true body cavity or cœlom; (2) there is no separate circulatory system, but this rôle is played by the gastrovascular cavity; (3) there is no respiratory system, respiration taking place over the whole surface of the body; (4) there is no skeletal system, all parts of the body being soft, without any hardened protective covering of any sort, and without any spicules.

C. Asexual Reproduction

Some species of Planaria, notably *P. dorotocephala*, rarely develop sexual organs. They have been reared in laboratory cultures for years without ever showing any gonads. Yet they reproduce quite effectively in another way. Large animals of a relatively mature age, when their activity has slowed down, undergo transverse fission, the fission plane being about at the level of the line *f—f* in Figure 127. The separated posterior piece pulls loose and

becomes a new animal, while the anterior portion regenerates a new posterior end. The posterior region contains not merely one individual, but there are several other potential individuals represented in it, as is indicated in the illustration by the lines drawn across the body.

A physiological explanation of the fission process has been given by ***Child***. The animal has a well-defined axiate organization, owing to the fact that the head, or apical end, is the region of highest metabolic activity. From the apical region there is a gradient of decreasing metabolic rate until the level *f—f* is reached. "There a sudden rise occurs, and then again a downward gradient toward the posterior end. The region where the rate rises suddenly represents the apical end of the second individual and the downward gradient following is the gradient of the major axis of this zoöid. In the shorter animals only one of the zooids is present, but as the length increases the basal body region may show two, three, or more distinct gradients (Fig. 127). Represented graphically, the metabolic gradient in such an animal is like the curve in Figure 128: *a* is the head region, the long slope the body of the anterior chief zoöid, which forms most of the body of the worm, *b* represents the apical point of the second zoöid, *c* that of the third, etc. These zoöids are the result of successive physiological isolations of the basal region as the animal grows in length."

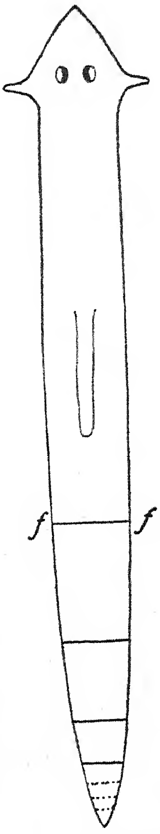


FIG. 127. *Planaria dorotocephala*, outline, indicating several zoöids in basal region; *f—f*, usual level of fission. (From Child.)

Certain principles involved in this situation need further elucidation. When a Planarian is young, it is relatively short and its whole body, especially the head, has a relatively high rate of metabolism. As it grows older it becomes longer and its whole metabolic rate slows down. When young, the high metabolic rate of the head was able to exercise a dominance, through the transmission of stimuli down the gradient, over the entire length of the animal. With a slowing down of the metabolic rate of the apical end and an increase in the length of the path over which

the impulse travels, there comes a time when the apical end can no longer maintain a physiological dominance over the entire axis. At the point where dominance fades out, an independent part of the body arises through what is known as PHYSIOLOGICAL ISOLATION. The isolated piece, the second zoöid, has its own gradient, the metabolic rate of the anterior end being the highest. This region now becomes a new apical end or, morphologically speaking, the head of a new zoöid. No structural indications of a new individual are visible, however, at this time. The only tests of the presence of a second or third individual are physiological tests. It has been shown in many ways that the metabolic gradients are as shown in Figure 128. Then, too, the posterior zoöid shows

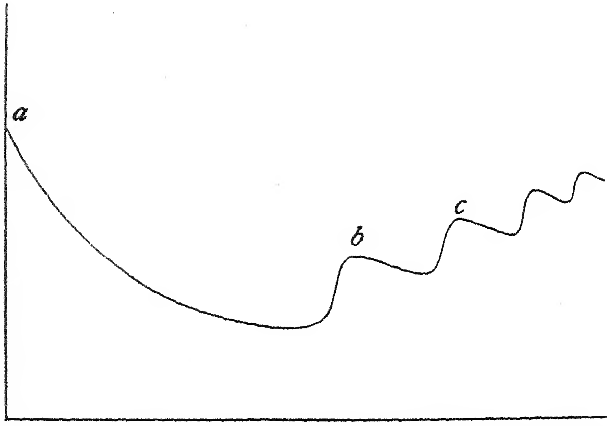


FIG. 128. Graphic representation of major axial gradients in a *planaria* with several zoöids. *a*, head of animal; *b*, *c*, apical regions of secondary zoöids. (From Child.)

lack of coördination with the rest of the animal, often holding on when the latter goes ahead. Thus the body becomes greatly stretched as in Figure 129 and sooner or later a separation occurs at the fission level, *f—f*. The isolated posterior zoöid now forms a new head, with eyes, brain, and other parts. The new head then reorganizes the rest of the piece into a complete new individual.

It is important to note that, even in flatworms like Planaria, there is a tendency for the animal to become a chain of individuals consisting of one dominant individual with a well-developed head and one or more subordinate individuals formed posteriorly.

In MICROSTOMUM, a flatworm belonging to the same class as Planaria, the production of a series of zoöids goes some steps further. Here the new individuals are morphologically differentiated but not completely cut off, since the alimentary tract remains continuous through the whole chain. Note (Fig. 130) a chain of sixteen zoöids more or less completely formed. The original head is seen at the top, with a large mouth, relatively large brain, eye-spots, and ciliated pits. None of the other individuals have eye-spots, nor so large a brain, nor a fully formed mouth. Evidently the first fission occurred about halfway back, for the apical end of this second zoöid has the brain rather large and a mouth broken through into the intestine. This evidently dominates all of the minor individuals of the posterior half. The third fission divided the anterior zoöid again, producing a third zoöid with a small brain and a mouth partly formed. The second zoöid then gave off the fourth zoöid posteriorly, which is somewhat less well developed than the third. Each of the first four zoöids is in process of dividing again, as shown by incipient mouths and fission planes across the body. Subsequently the series of individuals breaks apart and each zoöid becomes an independent worm. If the chain were to remain permanently under the dominance of the original head, we would have a condition in many respects similar to that seen in the Annelida (the

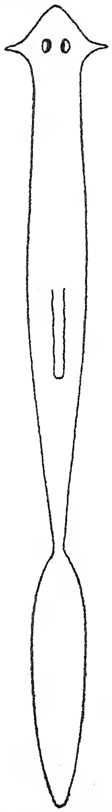


FIG. 129. *Planaria dorotocephala* in the act of fission. (From Child.)

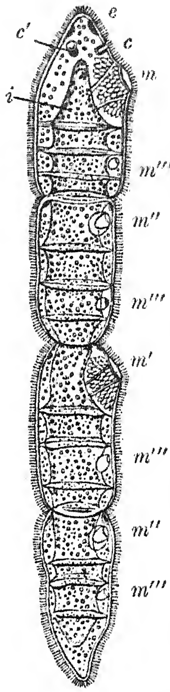


FIG. 130. Process of repeated fission in *Microstomum*. c, c', ciliated groove; e, eye-spot; i, intestine; m, m', m'', m''', mouths of primary, secondary, tertiary, etc., zoöids. Note that there are sixteen zoöids belonging to four grades. (From Parker and Haswell, after von Graff.)

segmented worms), which constitute the subject matter of our next chapter.

D. Regeneration in Planaria

It has been shown how Planaria can break its own body into two parts and regenerate a whole individual from each of the parts. Essentially the same thing takes place when with a sharp knife one cuts a Planaria into two pieces. The posterior piece constricts itself more or less at the cut surface and new colorless tissue forms over the wound. Out of this new tissue a small head is differentiated. The new head then takes command of the piece and reorganizes its materials into the body of a complete worm. Small pieces may be cut out of the worm at various levels of the primary axis. For example, pieces *a*, *b*, and *c* may be removed from a worm like that shown in Figure 131. This might be repeated in fifty worms and a comparison made of the average success in regeneration of *a*-pieces, *b*-pieces, and *c*-pieces. It is found that heads form nearly always in *a*-pieces, less frequently in *b*-pieces, and relatively rarely in *c*-pieces. Moreover, the heads that do form in *a*-pieces are normal, those in *b*-pieces frequently subnormal, and those in *c*-pieces mostly subnormal. This seems to indicate: first, that there is a gradient down the axis of the original worm, and second, that as one goes further down the axis there is less difference between the apical end and the basal end of the piece, so that it is difficult for the apical end to gain ascendancy over the rest of the piece and thus to produce normal apical structures.

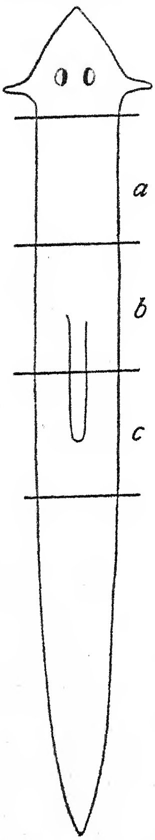


Fig. 131. Outline of *Planaria dorotocephala*, indicating regions, *a*, *b*, *c*, from which pieces are taken. (From Child.)

If a small piece is cut out very close to the head, there is so little difference in the rate of metabolism at the apical and basal ends of the piece that neither end dominates the other and a head is formed on both ends (Fig. 132). By artificially controlling the rate of metabolism of regenerating pieces it is possible to alter the prospective fate of

such pieces—to increase or to decrease the normal frequency of heads or the degree of normal development of heads and other parts. In brief, the interpretation of animal organization in terms of the rate of metabolism at different levels of the axis has en-

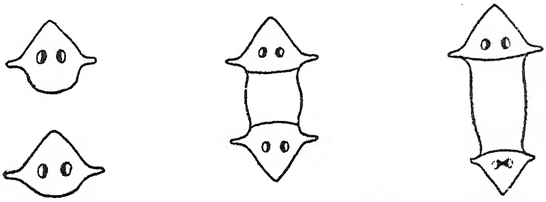


FIG. 132. Reconstitution of single and biaxial apical structures from short pieces of *Planaria*. (From Child.)

abled the experimenter to control development with a great deal of nicety, and to obtain results that have thrown much light on the nature of the processes of development and of reproduction.

E. Other Flatworms

The PHYLUM PLATYHELMINTHES consists of three classes:—

Class I. Turbellaria (Planarians, etc.).—Free-living, carnivorous, ciliated worms, with fairly well-developed head and sense organs.

Class II. Trematoda (Flukes).—Small, always parasitic flatworms, destitute of cilia and with a cuticle; having usually two sucking disks, and with head parts greatly reduced. This group is well illustrated by the common liver fluke (*Fasciola hepatica*), parasitic in the gall bladder of the sheep (Fig. 133). As compared with Planaria, it should be noted that the anterior or prepharyngeal part of the body has been greatly shortened, so that almost the whole body corresponds to the postpharyngeal part of Planaria. The mouth, provided with a sucker, is anterior in position and opens into a two-branched digestive tract. The second sucker, which is for attachment only, is on the ventral side near the anterior end. The reproductive system is even more complex than in Planaria. A remarkable and characteristic peculiarity of the flukes is their complicated life history. In addition to the fact that they have a long series of larval generations between the egg and the adult, they spend part of the life cycle in the body of an intermediate host, a water snail. The life cycle is represented in the accompanying illustration (Fig. 134).

Eggs in large numbers are fertilized in the body of the adult fluke, are given off into the bile duct of the sheep, pass out through the digestive tract, and are voided with the fæces. The egg hatches out when it rains and a tiny ciliated aquatic larva, the MIRACIDIUM (Fig. 134, **A**), emerges and, if lucky, finds a snail of the genus Lymnea, into whose body it bores. Here it rounds up into a saclike thing called the SPOROCYST. Some of the cells of the sporocyst appear to be parthenogenetic ova, each of which develops into a larval form much more elaborate than a miracidium, called a REDIA (Fig. 134, **C**), which has a definite alimentary canal and two processes, like paired legs, on the outside of the body. The rediæ break out of the sporocyst and, in turn, produce parthenogenetic ova that develop into more rediæ. This is repeated for several generations. Then some of these later rediæ give rise parthenogenetically, as before, to a generation of still more advanced larvæ called CERCARIÆ (Fig. 134, *C*). Each cercaria is shaped something like a tadpole, but with flattened body and long swimming tail (Fig. 134, **D**). It is a true larval form which changes without further multiplication into an adult fluke. The young cercaria bores its way out of the snail's body, loses the tail, and rounds up into a cyst. These cysts are eaten by grazing sheep and the cyst is digested off, releasing the young fluke in the stomach or intestine, whence it finds its way to its favorite abode, the gall bladder. There it attaches itself and grows up to the adult condition.

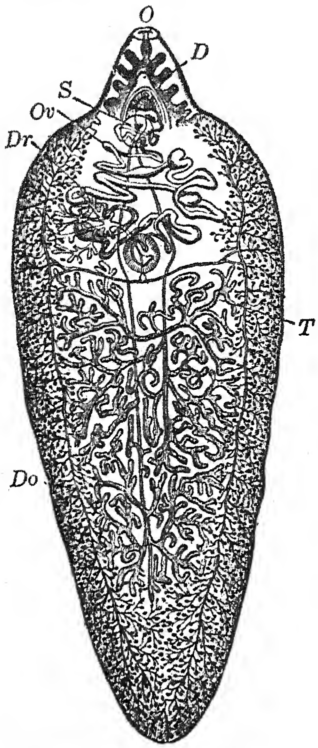


FIG. 133. The liver fluke, *Fasciola hepatica*. *D*, anterior part of intestine (posterior part not shown); *Do*, yolk-glands; *Dr*, ovary; *O*, mouth; *Ov*, uterus; *S*, sucker; *T*, testes. (From Sedgwick, after Sommer.)

Class III. Cestoda (Tapeworms).—Internal parasites with a complex life history involving two hosts. They are extremely de-

generate forms, with no mouth nor digestive tract. The original young BLADDER WORM multiplies by transverse fission, producing a long ribbonlike series of secondary individuals (PROGLOTTIDES), which are little more than bags of reproductive organs.

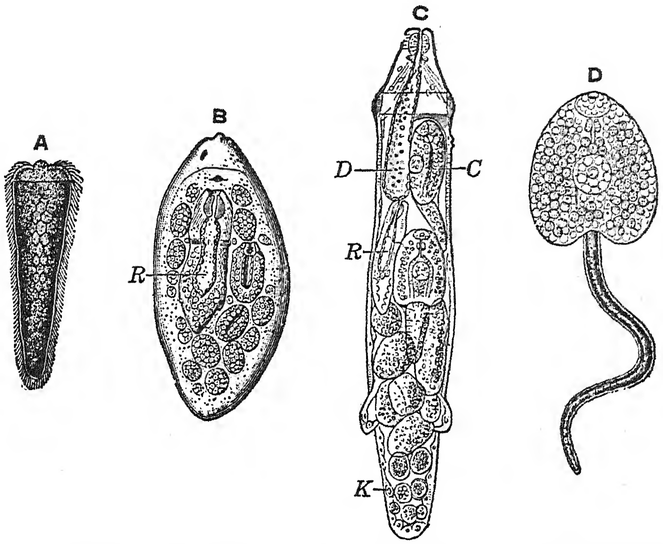


FIG. 134. Stages in the life-history of the liver fluke, *Fasciola hepatica*. A, miracidium (ciliated embryo). B, sporocyst containing rediæ (*R*). C, a redia; *C*, cercaria; *D*, gut; *K*, germ cells; *R*, redia. D, cercaria. (From Sedgwick; B, after Leuckart; C and D from Hegner, after Thomas.)

An example of the Cestoda is a common tapeworm of the human intestine, *Tænia solium* (Fig. 135). The adult animal (A) consists of a headlike anterior part, called the SCOLEX (B), which is provided with a ring of hooks (C) and several suckers. Behind the scolex is a short part called the NECK, and this is followed by a long series of rectangular flattened individuals, proglottides, which are smallest next to the neck and largest at the posterior end. A single worm may be ten feet or more in length and contain nearly a thousand proglottides. New proglottides are constantly being produced from the neck region, so that those farthest from the neck are the oldest. The larger proglottides are sexually mature and seem to be practically filled with reproductive organs of both sexes. The long, tapelike series of proglottides becomes folded one part against another, bringing the proglottides together

in pairs so that they are able to effect a mutual exchange of spermatozoa. The fertilized eggs develop while in the uterus of a

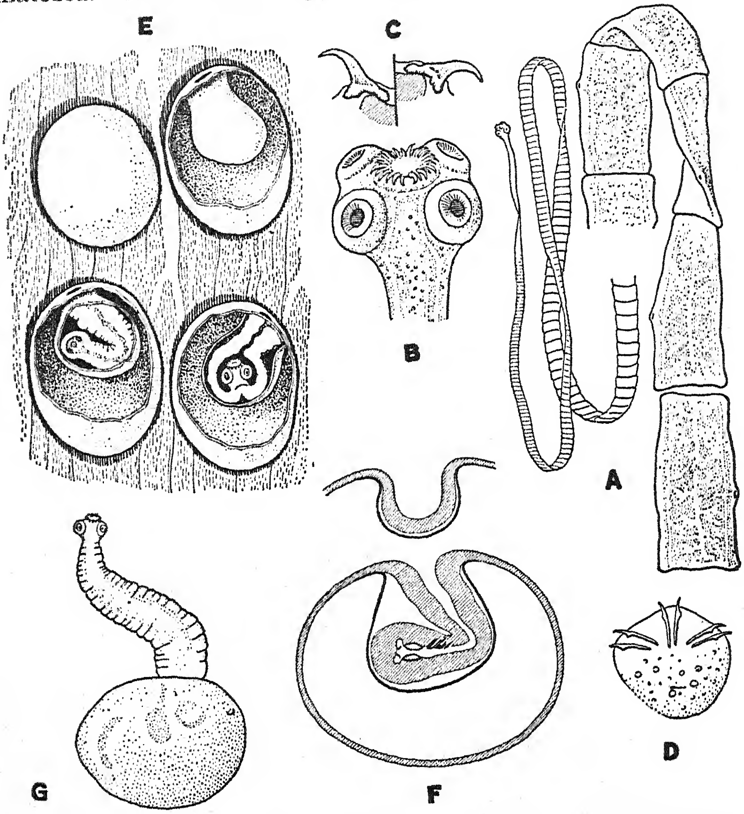


FIG. 135. The human tapeworm, *Tænia solium.* A, shows representative portions of a single tapeworm including the scolex, the region of fission, many young proglottides, and a few sexually mature proglottides, the posterior one being the oldest and now free. B, the scolex enlarged, showing the four suckers and the apical crown of hooks. C, separate hooks showing method of grasping. D, hexacanth, or six-hooked embryo. E, a group of bladder worms (cysticerci) embedded in the muscle fibers of the hog. F, shows two stages in the invagination that results in the bladder-worm condition. G, bladder worm with head evaginated and ready to attach itself to the wall of the human intestine. (Redrawn after Pfurscheller wall chart.)

proglottid into small spherical embryos armed with six hooks (D). Proglottides, laden with these embryos, break off and pass out of the body of the host along with fæces. Hogs pick up the pro-

glottides as the result of filthy feeding habits. The proglottides are digested in the alimentary tract of the hog, and the freed embryos work their way through the walls of the alimentary tract, reach their destination in the voluntary muscles, in the liver, and in other organs, where they become encysted, and during encystment develop into BLADDER WORMS with inverted heads (E and F). If underdone pork infested with these parasites be eaten by man, some bladder worms (CYSTICERCI) are released in the intestine. Each bladder worm shoots out its hooked head (as in G) and attaches itself to the wall of the intestine. The bladder is soon lost and the series of transverse fissions ensues, giving rise to another chain of proglottides.

This process of multiplication by transverse fission doubtless has the same physiological basis as has the formation of zoöids in Planaria. It begins, however, while the worm is still an embryo, or at least no more than a larva. This is significant, because it has some points of resemblance to the formation of metameres or segments in the Annelida.

SUMMARY

1. Planaria belongs to the Phylum Platyhelminthes and the Class Turbellaria, which are nonparasitic, carnivorous, ciliated flatworms with well-developed preoral body region and definite head.

2. Planaria resembles the medusa forms of the cœlenterates in having mouth but no anus, a gastrovascular cavity, a proboscis-mouth near the center of the body (but the oral-aboral axis of the medusa becomes the ventrodorsal axis of Planaria), and in carrying on intracellular digestion.

3. Planaria has a new primary axis, the anteroposterior axis, apparently derived by specialization of one of the radii of the radial axes of the cœlenterate-like ancestor.

4. Bilateral symmetry, another new development, may be a result of a secondary pairing of the rest of the radial axes of the ancestral form.

5. Another new feature in Planaria as compared with Hydra is the mesoderm, which is in the form of loose packing tissue called by some biologists mesenchyme, for they do not regard it as true mesoderm.

6. Planaria has single-celled excretory organs, called flame cells.

7. The central nervous system consists of two cephalic ganglia, two wide-apart ventral nerve cords. With the "brain" are associated eye-spots and auricles (or tentacles), the chief sense organs.

8. Flatworms are hermaphroditic, and like most hermaphrodites, have a very complex reproductive system with many specialized accessory organs.

9. Asexual reproduction takes place by cutting off the posterior end to form a new zoöid. The physiological explanation of this is that, according

to the gradient theory, the parts most remote from the apical region of the axis, fail to receive strong integrational impulses from the head and tend to become independent. This gives rise to a new apical region and a new individual.

10. Some flatworms form chains of individuals temporarily dominated by the anterior zoöid. The zoöid theory of metamerism in the annelid worms holds that such temporary chains came to be more closely integrated and produced primitive annelids.

11. Like Hydra, Planaria has been extensively used in the study of regeneration. Small, severed pieces of Planaria are capable of regenerating to form whole individuals. A severed piece must first form a new head and this acts as an organizer of the living material, and controls its development into a new individual like the parent.

12. The complex life history of the liver fluke (Phylum Platyhelminthes, Class Trematoda) involves several larval generations reproducing parthenogenetically and pædogenetically.

13. The tapeworm (Phylum Platyhelminthes, Class Cestoda) shows extreme degeneration of those organs and systems important in free, independent living. A so-called tapeworm is really a linear series of zoöids, temporarily joined together and each self-sufficient. Like many other parasites, part of the life cycle is passed in one host and part in another.

in turn, reflects the asymmetry of the visceral mass. The first shell of the young snail is retained as the apex of the permanent shell, and new and broader rings are added by the mantle edge as the animal grows larger and larger. On account of the more rapid growth of one side of the body, the shell assumes the form of a true spiral coil.

2. *Internal Anatomy of the Snail*

a. The Digestive Tract.—Anteriorly, the mouth, which has a horny jaw in front, opens into the BUCCAL MASS, which consists of the RADULA (a filelike ribbon used for shredding the food before swallowing) and the RADULA SAC, together with its muscles and

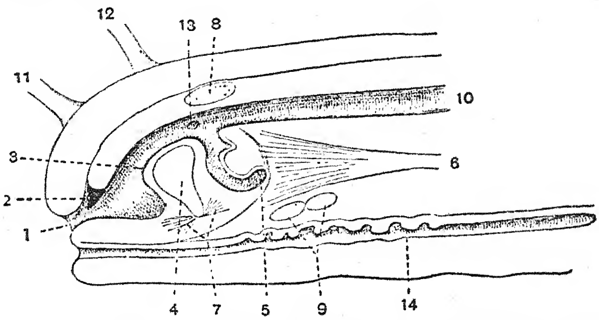


FIG. 151. Inner view of right half of head of *Helix*, showing the arrangement of the radula. 1, mouth; 2, horny jaw; 3, radula; 4, cartilage supporting radula; 5, radula sac from which radula grows; 6, muscle which retracts the buccal mass; 7, intrinsic muscles that rotate the radula; 8, cerebral ganglion; 9, pedal and visceral ganglia; 10, œsophagus; 11, anterior tentacle; 12, eye tentacle; 13, orifice of the duct of salivary gland; 14, mucous gland which runs along the foot and opens just under the mouth. (From Shipley and MacBride.)

cartilage (Fig. 151). Behind this is the œsophagus, which soon widens into the stomach (Fig. 153). Lying against the stomach are two large SALIVARY GLANDS that pour their secretion into the BUCCAL CAVITY. The rest of the digestive tract is long and slender and more or less coiled. The posterior part of it is directed forward toward the head and it ends in the ANUS, which opens on the left side just back of the mantle cavity. A large digestive gland, usually called the LIVER, occupies a considerable portion of the visceral hump and pours its secretion into the intestine.

b. Nervous System.—The central nervous system, like that of the annelids, is composed of paired ganglia, each of which is the

nerve center of some important function or set of functions (Fig. 152). In a very real sense, each pair of ganglia is a brain; but they are all connected by means of commissures and are therefore not independent of each other. The two largest ganglia are, as in the annelids, situated above the œsophagus and are known as the CEREBRAL GANGLIA; they may well be called the principal brain, while the other ganglia mentioned below are secondary or subordinate brains, each presiding over some region of the body under the general superintendence of the principal brain. Beneath the œsophagus is a rather compact nervous mass composed of several pairs of ganglia (PEDAL, PLEURAL, PARIETAL, and VISCERAL) that are connected by means of pairs of commissures on either side of the œsophagus with the cerebral ganglia. A very small pair of BUCCAL GANGLIA is connected by means of its own commissures with the cerebral ganglia.

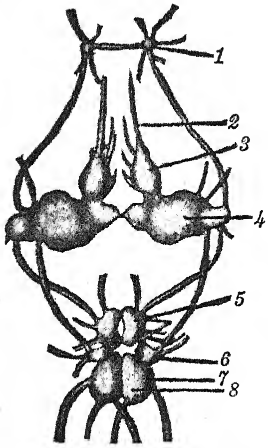


FIG. 152. Central portion of the nervous system of *Helix pomatia*. *1*, buccal ganglion; *2*, optic nerve with thickened root (*3*) arising from the cerebral ganglion (*4*); *5*, pedal; *6*, pleural; *7*, parietal; *8*, visceral ganglion. (From Lang, after Böhmig and Leuckart.)

c. Reproductive System.—Many snails have extremely elaborate reproductive systems, for they are hermaphroditic, having in one individual all the organs of both sexes. In spite of this they do not fertilize their own eggs but merely exchange sperms somewhat after the fashion described for the earthworms. Other snails are diœcious, that is, they have the sexes separate. Each individual of the hermaphroditic species, such as *Helix pomatia* (Fig. 153), has the following male organs: TESTIS, VAS DEFERENS, PENIS, DART SAC, and various accessory glands. Each individual has also the following female organs: OVARY, OVIDUCT, ALBUMEN GLAND, VAGINA, and several minor structures. In complexity this type of reproductive system rivals that of the flatworms.

d. Circulatory System.—This system differs from that of the annelids, vertebrates, etc., in that it is not a closed system of vessels, but an open system. By this we mean that the heart pumps blood through a few main arteries and arterial capillaries, which,

in turn, pass the blood into venous capillaries. These instead of uniting directly into veins, open into a system of sinuses that penetrate all the tissues and bring the blood into intimate contact with the cells. Blood returns to the heart after traversing a series of

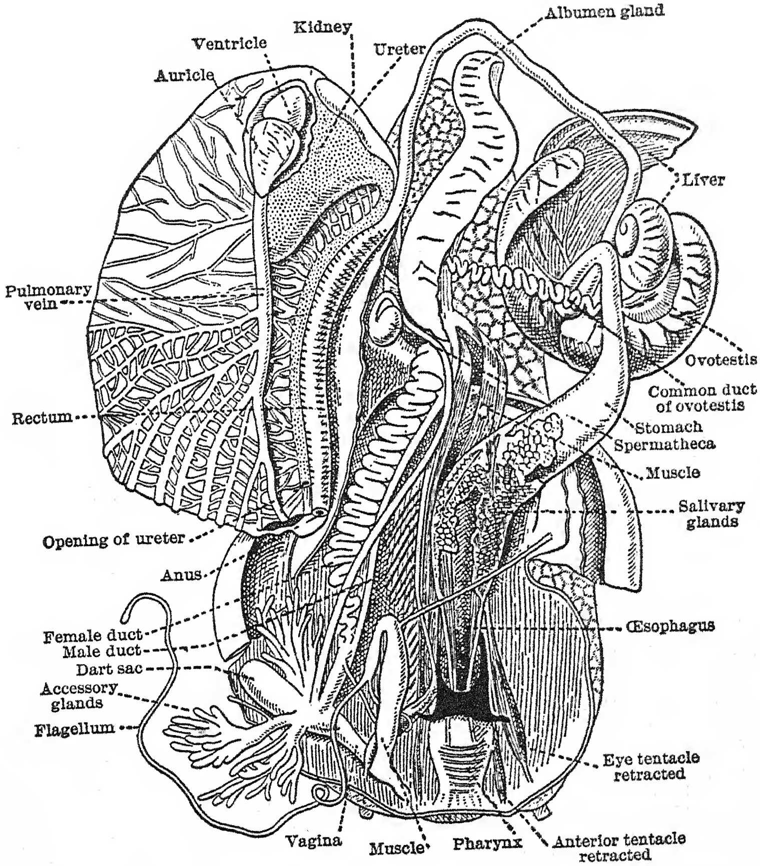


FIG. 153. Internal anatomy of *Helix pomatia*. (From Hatschek and Cori.)

veins (pulmonary veins) in the mantle roof. The heart lies in a cavity (PERICARDIUM) which corresponds to the cœlom of other groups and is not homologous with the pericardium of the arthropods, for the latter is a blood sinus.

The other systems of the snail are less distinctive and will not be described here.

3. *Activities of the Snail*

a. Homing Instinct.—Perhaps the most remarkable of the snail's activities are those associated with its strong instinct to maintain a fixed headquarters, or base of operations. Snails are, for the most part, nocturnal in their activities and need to seek a sheltered retreat during the day. As a rule, snails or slugs make excursions of considerable extent in search of food, but in spite of their varied wanderings they appear always to return to the same home retreat at the approach of day. One observer noted that a snail, which he had taken the precaution to mark with a spot of white paint, occupied a hole at some distance from the ground in a brick wall. Leaning against the wall with its end near the hole was a stick, the lower end of which rested among the herbs of the garden. As soon as it began to grow dark the snail habitually came down this improvised ladder and, after feeding over a considerable area during the night, always returned to and ascended its ladder and was at home by the first break of dawn.

b. Sense of Smell.—The snail has an exceedingly keen sense of smell, as is well illustrated by the following incident described by ***Furtado:*** "He noticed a *Helix adspersa* lodged between a column on a veranda and a flower-pot containing a young banana plant, and threw it away into a little court below, and six or seven yards distant. Next morning the snail was in precisely the same place on the flower-pot. Again he threw it away, to the same distance, and determined to notice what happened. Next morning at nine o'clock, the snail was resting on the rail of the staircase leading to the veranda from the court; in the evening it started again, quickening its pace as it advanced, eventually attacking the banana in precisely the same place where it had been gnawed before." Presumably the scent of the banana had guided the snail over a somewhat intricate path. Authorities agree that the sense of smell has its seat in the tentacles and that this sense is the snail's main dependence.

c. Tenacity of Life.—Land snails, especially those that live in arid regions, exhibit an almost unbelievable tenacity of life. One author states that he glued two specimens of *Helix desertorum* to a tablet in his collection of shells, and four years later, on reëxamining this case of shells, he found one of the snails alive and healthy but ravenously hungry. Many other cases are on record of snails

surviving without food or water for periods of from two to six years. Doubtless their ability to seal themselves almost hermetically within their shells by means of the operculum accounts to some extent for their ability to avoid desiccation.

C. The Clam

1. *General Features*

The clam is a representative of a very large and important class of Mollusca, Pelecypoda, which includes oysters, scallops, and other important food animals. For reasons that are not difficult to understand, the clam is generally chosen as the type of Mollusca for laboratory use. These animals are easily obtained, of convenient size, and may readily be kept alive in aquaria. Except for these practical advantages, they are singularly ill suited to illustrate the characteristics of the Phylum Mollusca, for they are essentially degenerate, headless forms.

The Pelecypoda seem to have been one of the earliest of the molluscan groups to reach the end of their evolutionary progress, if their history may be called progress, for we find their fossil remains in almost the earliest fossil-bearing strata. These ancient clamlike mollusks were essentially as specialized as are the modern types.

The characteristics of the Class Pelecypoda are as follows: They have bivalve shells, sheetlike gills, a wedge-shaped foot, and extremely reduced head. They are all aquatic in habitat. They range in size from tiny forms that in the adult state are no larger than a pinhead up to giant clams over three feet in shell length and weighing 500 pounds.

For the most part clams are burrowers and trenchers. Many species burrow about in mud or even excavate tunnels in soft rock. Some specialized forms such as the shipworm, or teredo, have the habit of excavating passageways in submerged wood, using the wood for food. In this way they riddle with their tunnels wharfing piles and the hulls of ships, causing an annual loss of many millions of dollars.

The common fresh-water clam, or mussel, may be a surface trencher as well as a burrower. In some regions they seem to prefer to move about over the surface of the muddy bottoms. As the animal moves slowly about on its plowshare-like foot it leaves a

furrow. Often in quiet waters the bottom is sculptured with a labyrinth of these clam paths.

Moving about slowly as they do, they could not well capture active prey. Instead, they have adopted a scheme used by many other sedentary or semisedentary aquatic organisms: that of concentrating the organic particles suspended in all natural waters. The surface of the body, and especially that of the voluminous curtainlike gills, is covered with cilia that whip the water into currents and focus the streams into grooves that lead ultimately into the troughlike lips of the mouth, the so-called LABIAL PALPS. Feeding seems to be practically a continuous process and is intimately associated with respiration, for the steady current of fresh oxygen-bearing water serves admirably as a respiratory medium.

2. *Anatomy of the Clam*

a. General Description.—The clam is constructed more or less like a book. The two shells are like the covers; the hinge like the

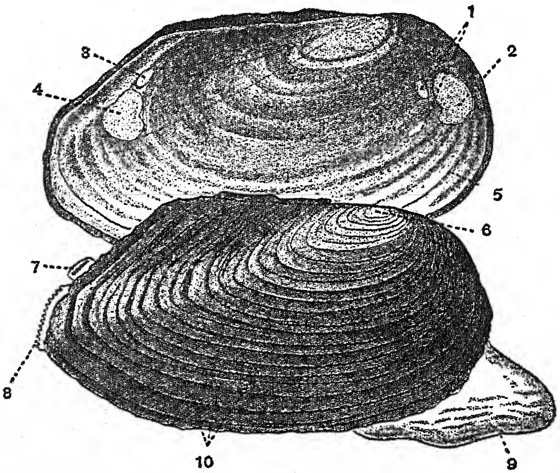


FIG. 154. Shell containing clam, *Anodonta mutabilis*, and behind it an empty left shell. 1, 2, attachment of anterior muscles; 3, 4, attachment of posterior muscles; 5, line of growth; 6, umbo; 7, dorsal siphon; 8, ventral siphon; 9, foot; 10, lines of growth. (From Shipley and MacBride.)

book back; the mantle folds like the pages pasted to the covers; the gills like the double fly leaves, front and back; while the body of the clam corresponds roughly to the body of the book, except that it is not divided up into pages.

Unlike the snail, the clam is bilaterally symmetrical. With a sharp instrument it is possible to sever the body into two equivalent halves, each a mirror image of the other.

The shell (Fig. 154) consists of two VALVES united dorsally by an elastic HINGE. The concentric rings seen on the outside of the shell are LINES OF GROWTH. A new ring is added to the outer margin each season. The original shell of the young clam, though usually worn and eroded, may be seen in the center of the UMBO, the somewhat elevated area situated dorsally and near the anterior end of

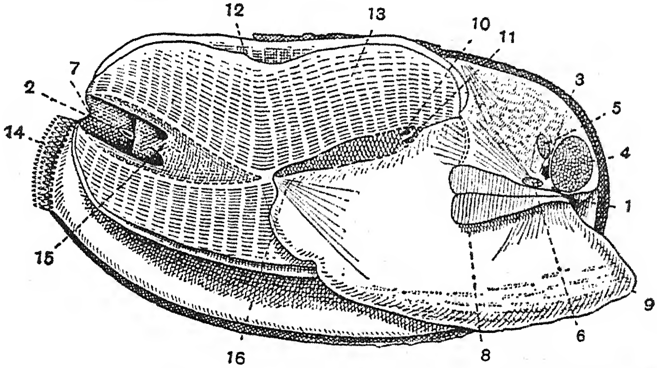


FIG. 155. Right side of *Anodonta* with the right mantle cut away and the right gills folded back. 1, mouth; 2, anus; 3, cerebropleural ganglion; 4, anterior adductor muscle; 5, anterior protractor muscle; 6, retractor muscle; 7, dorsal siphon; 8, inner labial palp; 9, foot; 10, opening of nephridium; 11, opening of genital duct; 12, outer right gill; 13, inner right gill; 14, ventral siphon; 15, epibranchial chamber; 16, posterior protractor muscle. (From Hatschek and Cori.)

the shell. The shell is three layered: the outside layer being horny, or chitinous; the middle layer being composed of crystals of calcium carbonate and of considerable thickness; the inner, or mother-of-pearl layer, being relatively thin and made up of a number of delicate sheets of nacreous material that has an iridescent appearance.

The muscles of the shell are used for closing the shell. These are two in number, the ANTERIOR and POSTERIOR ADDUCTORS. The shell opens automatically owing to the elasticity of the ligamentous hinge. This accounts for the fact that the shells of dead clams are widely open.

The MANTLE (Fig. 156) consists of two extensive folds of the body wall that come off from the dorsal part of the body and

envelop the body proper. These mantle folds secrete the shell and also function after the manner of washers in a valve, enabling the shell to close up in water-tight fashion. Two regions of the mantle margin are specialized into two more or less elongated tubes, or siphons, the DORSAL and VENTRAL SIPHONS. These are openings through which water enters the mantle cavity and makes its exit, the ventral siphon taking in water and the dorsal siphon expelling it. In some clams, such as the little neck clam, these siphons become very much elongated so as to enable the clam, even when buried some depth in the mud, to continue respiration and feeding uninterrupted.

The GILLS, or BRANCHIÆ (Fig. 155), are four in number. They hang down into the mantle cavity like curtains, two being suspended by their dorsal margins on each side of the body. They have a very elaborate sievelike structure, designed to present a vast amount of surface with relatively little bulk, an ideal arrangement for respiratory organs.

b. Digestive System (Fig. 156).—The digestive system consists of a MOUTH situated near the dorsal part of the foot between the two pairs of flaplike LABIAL PALPS. Each pair on one side is united along the inner edges to form a trough leading into the mouth. Cilia lining these troughs sweep the food particles, already concentrated by the gills and other organs, into the mouth. Next to the mouth is the very short ŒSOPHAGUS that in turn opens into a fairly large STOMACH. The latter opens into a long coiled INTESTINE, that takes several turns through the tissues of the dorsal part of the foot, passes through the PERICARDIUM, and opens to the outside through the ANUS that lies near the dorsal siphon. The two lobes of the LIVER practically surround the stomach and furnish it with a digestive secretion.

c. Excretory System.—In the clam there is but one pair of U-shaped kidneys (NEPHRIDIA) that lie one on each side of the pericardium and discharge their waste products through two renal apertures near the dorsal siphon, whence it is carried away by the outgoing water currents.

d. Nervous System (Fig. 156).—A number of widely separated pairs of GANGLIA, connected by COMMISSURES comprise the nervous system. The BRAIN, if a headless creature may be said to possess a brain, consists of a pair of ganglia, the CEREBROPLEURAL GANGLIA, one on each side of the œsophagus and connected by a com-

missure that passes above the œsophagus. Two other pairs of ganglia are connected with the cerebropleural ganglia by means of commissures, namely, the PEDAL GANGLIA situated in the foot and controlling its activities, and the VISCERAL GANGLIA situated near the posterior adductor muscle and controlling the visceral functions. Minor ganglia are associated with the action of the chief muscles.

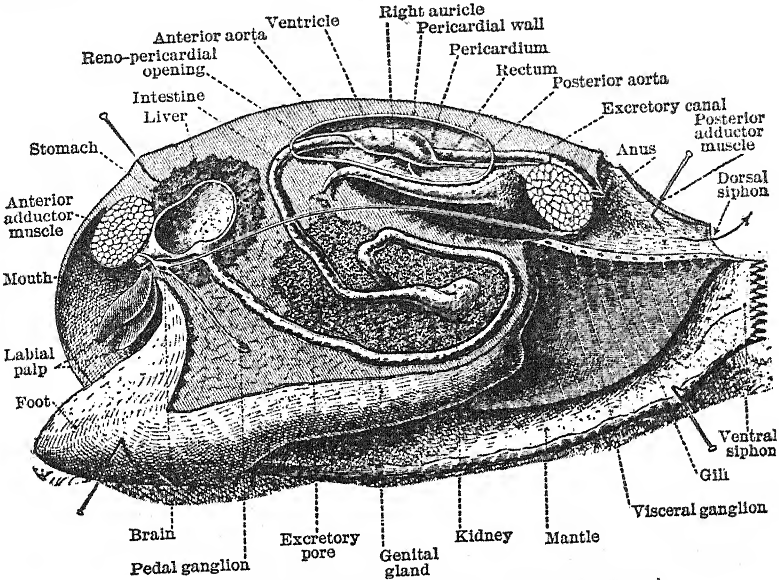


FIG. 156. Internal anatomy of a clam. (From Jammes.)

e. Circulatory System (Fig. 156).—The circulatory system consists of a HEART lying in a saclike sinus, the pericardium, ARTERIES, VEINS, and an elaborate system of blood spaces, or SINUSES. In general, it does not differ essentially from that of the snail which has already been described.

Other anatomical details may best be studied in the laboratory.

D. OTHER MOLLUSCA

There are five classes of mollusks:—

Class I. Amphineura—chitons, a group of primitive mollusks not unlike the snails, but differing from the latter in being bilaterally symmetrical. They usually possess a compound dorsal shell

composed of eight transverse calcareous plates overlapping like shingles. Although obviously degenerate in some respects, they appear to be more nearly like the ancestral mollusks than any other group of the present day.

Class II. Gastropoda—land snails, sea snails, whelks, etc. This group, although bilaterally symmetrical as to head and foot, shows pronounced asymmetry of the mantle, shell, and visceral mass. The other characters of this class have already been described.

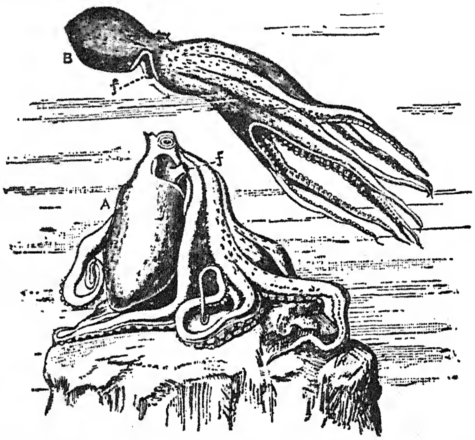


FIG. 157. The octopus, *Octopus vulgaris*. A, at rest; B, in motion. *f*, funnel; the arrow shows direction of propelling current of water. (From the Cambridge Natural History, after Merculiano.)

Class III. Scaphopoda—toothshells. This is a small group of degenerate mollusks with tubular shell and mantle, boring foot, and bilateral symmetry.

Class IV. Pelecypoda—clams, oysters, scallops, etc. This group is characterized by bilateral symmetry, a shell composed of two hinged valves, a two-lobed mantle, sheetlike gills, a plowshare foot, and practically no head.

Class V. Cephalopoda—squids, cuttlefishes, octopi (Fig. 157), and nautili. They are bilaterally symmetrical. The head and foot combine to make a secondary head armed with tentacles and provided with eyes that are superficially like those of fishes. The various pairs of ganglia are closely fused together to form a rather large, compact brain. These animals are apparently as advanced in their organization and as capable in every way as are fishes; in some respects they seem to be superior.

E. Affinities of Mollusks

Although quite unlike annelids in the adult condition, mollusks show a remarkable resemblance to annelids in their early develop-

mental stages. The elaborate pattern of early cleavage is almost the same in the two phyla and they both have a trochophore larval stage. In the mollusks, however, a second larval stage (veliger larva) intervenes before the adult form is reached. These facts indicate that mollusks and annelids have been derived from a common ancestor and belong close together on the phylogenetic tree (Fig. 83).

SUMMARY

1. Mollusca are nonmetameric; have greatly reduced cœlom; have an open circulation (the blood flowing from capillaries into intricate blood sinuses); the body consists of four main parts, head, foot, mantle, and visceral mass; they have typically first, a trochophore larva and later, a veliger larva.

2. The snail belongs to the Phylum Mollusca and the Class Gastropoda, which is characterized by bodily asymmetry and usually a single shell, spirally coiled.

3. The asymmetry is due to the more rapid growth of one body half, resulting in a spiral coiling of the visceral mass and a general one-sidedness of organization.

4. The central nervous system consists mainly of a pair of ganglia (brains) for each body part, consisting of cerebral, pleural, pedal, parietal, and visceral ganglia, connected to each other by nerve commissures.

5. There is a well-defined heart with valves (ostia) opening into a large pericardial sinus, that is a vestige of the cœlom.

6. The clam belongs to the Phylum Mollusca and Class Pelecypoda, characterized by bivalve shells, sheetlike gills, wedge-shaped foot, and greatly reduced head. They are as a rule bilaterally symmetrical.

7. The whole body is enveloped in the paired mantle folds, which also secrete the paired valves of the shell.

8. The other classes of mollusks are Amphineura, Scaphopoda, and Cephalopoda.

9. Since the mollusks and annelids have very similar developmental histories up to a trochophore stage, they are believed to have been derived from a common ancestral group in which metamerism had not yet appeared.

10. The mollusks show what a high degree of specialization may be attained without employing the method of metamerism. They are the most specialized of the nonmetameric groups.

11. There are strong evidences that Mollusca are related to Annelida.

CHAPTER XXIV

THE GREAT PHYLUM ARTHROPODA

THE name, ARTHROPODA, is derived from two Greek words: *arthron*, a hinge, and *pous*, a foot. Thus all animals with jointed or hinged appendages, except the vertebrates, are placed in this phylum. In numbers of species and of individuals the arthropods outnumber all the other phyla combined. Over seven hundred thousand species of arthropods have been described, and there is reason to believe that at least that many more are still unidentified.

The phylum is one of immense antiquity, having representatives in the Cambrian rocks, whose age is estimated as about three hundred millions of years. The earliest arthropods were marine forms known as TRILOBITES, which must have been very numerous, judging by the abundance of their fossil remains. Like the mollusks, they serve as important time markers for the geologist.

It is customary to divide the arthropods into two great series, the first of which is adapted to aquatic life and usually possesses gills, and the second of which is adapted to terrestrial life and possesses a variety of air-breathing organs. The first division includes only the CLASS CRUSTACEA; the second comprises the CLASSES ARACHNIDA, ONYCHOPHORA, MYRIAPODA, and HEXAPODA (the insects). Any detailed survey of the above groups will show that the criterion used in defining the two series is only valid in a broad way; for there are terrestrial crustaceans and there are aquatic arachnids and insects.

A. GENERAL CHARACTERISTICS

a. Adaptive Radiation.—As in the case in all large and successful groups of animals, the Crustacea, Arachnida, and the insects have developed a very wide range of adaptations enabling them to occupy a multiplicity of habitats. Thus the Crustacea, the most successful of which are marine, have also invaded the fresh waters; while many of them, such as wood lice and pill bugs, have succeeded in adapting themselves for life in the air, but are limited to damp places. Similarly, the insects, which are preëminently

terrestrial, not uncommonly live on the surface of or beneath the surface of water. In addition to this, they have most successfully invaded the air and are rivals of the birds and the bats in this domain. Many of the insects have also adapted themselves to subterranean life; witness the seventeen-year locust (Cicada) that lives for sixteen years as a grublike larva, burrowing underground and feeding upon the roots of plants and trees, emerging as a full-fledged winged adult only during the summer of the seventeenth year (Fig. 158). Many insects, too, live parasitically on or in the bodies of other animals or plants, and it is this parasitic tendency that lends the group a very special economic importance. The Arachnida do not fall far short of the insects in the range of their adaptive radiation. Their particular specialties are those that are associated with the capture of prey. Thus the spiders build many sorts of snares and traps, that appear to be most ingenious. Some of the spiders also have succeeded in living under water, notably those that build miniature diving bells out of silk, which they anchor to the bottom and fill with air by carrying air bubbles trapped amidst the thick hair of the abdomen. These and many other instances serve to illustrate the almost universal application of the principle of adaptive radiation.

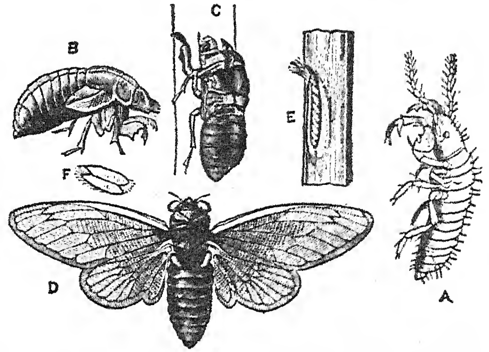


FIG. 158. Seventeen-year locust, *Cicada septendecim.* A, larva. B, nymph. C, nymph skin after emergence of adult. D, adult. E, section of tree showing how eggs are laid. F, two eggs enlarged. (From Sedgwick's Zoology, after Riley.)

b. Metamerism.—One of the most general features of the Arthropoda is that they, like the annelids and the vertebrates, are built on the segmental or metameric plan (Fig. 159). In contrast with the annelids, the number of segments is small, and in some higher groups is strictly limited to twenty-one (twenty, according to some authorities). The various metameres, or segments, are much more highly specialized and diversified than is the case in

the annelids, and in many of the arthropods secondary fusions of groups of adjacent segments have taken place in such a way as to leave the original metameric arrangements rather obscure. As a rule, each metamere is provided with a pair of jointed appendages; these are modified in all sorts of ways and for all sorts of purposes. Thus some are used as sense organs, others as mouth parts for holding or masticating food, others for walking, swimming, or even as copulatory organs. No better material for the study of the principle of homology, and especially of serial homology, could well be found than is afforded by the arthropods. This subject is to be dealt with in detail in the next chapter.

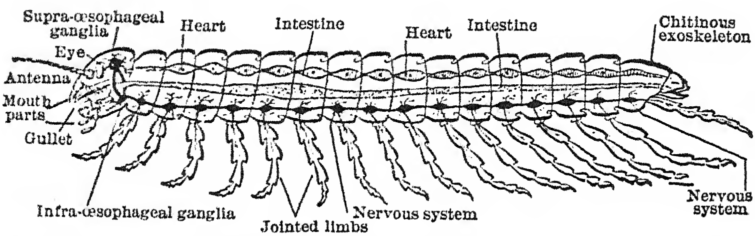


FIG. 159. Diagrammatic representation of the structure of an Arthropod. (From Schmeil.)

c. Exoskeleton.—The arthropods have no bones nor any true internal skeleton; but they are, as a rule, covered with a hard external armor secreted by the skin and composed of a horny material known as CHITIN. This exoskeleton is molded to the body and fits its every contour. It is, however, not equally hard all over, for this would render the animals entirely rigid; instead, it is soft at those regions where flexibility is necessary, namely, at the limb joints and between segments of the body armor.

d. Ecdysis.—An animal with an unyielding casing over the body cannot, of course, grow as other animals grow. The arthropods solve the problem of growth in a curious way. At intervals the armor is shed, and rapid expansion takes place during the period before another coat of armor is acquired and while the body surface is soft. The process of shedding the armor, ecdysis, is a strenuous and precarious one. The animal has first of all to loosen itself from all contact with the armor by a process of shrinking; then, by muscular expansion it splits the investment at certain definite weaker points; and finally, with a great effort it withdraws each

appendage from its individual casing, parts of large dimensions sometimes being pulled through comparatively small openings. This is hard and dangerous work and not infrequently involves the loss of life or at least of limbs. Moreover, the period during which the shell is soft is one when there is great danger from predaceous enemies. It should be said that the above description of ecdysis applies particularly to the higher crustacea, but that the process in some form is characteristic of all groups of arthropods.

e. Nervous System.—The central nervous system of the arthropods follows the same structural lines as that of the annelids, but is regionally modified and specialized to a much greater extent, just as are other metameric systems. The brain, CEREBRAL GANGLIA, as in annelids and mollusks, is above the œsophagus and is connected by paired commissures, one on each side of the œsophagus, with a pair of SUBŒSOPHAGEAL GANGLIA. Behind this there are the PAIRED NERVE CORDS with PAIRED SEGMENTAL GANGLIA, which are at intervals fused together into larger nervous masses that serve as secondary brains.

f. Sense Organs.—The eyes of arthropods are either simple or compound. In the more primitive members of the phylum very simple eyes, derived from the ectoderm, are found. Such an eye consists of a simple lens-shaped, transparent thickening of the cuticle, a number of retinal sensory cells, and a nerve running to the brain. In the case of the compound eyes groups of visual cells are separated from each other by wall-like boundaries, and each has a lenticular thickening of the cuticle. Each of the facets of such an eye receives a clear image of that part of the visual field directly in front of it. If the object or the insect moves the image shifts in the eye, giving information as to direction and nearness of the object.

g. Circulatory System and the Cœlom.—In most animals the circulatory system consists of a closed system of tubes, varying in caliber from large arterial trunks to the minutest capillaries, which carry the blood from the heart to all the tissues of the body and back again to the heart without allowing it to escape the confines of walls except by processes of diffusion. In the arthropods, however, as we have already said for the mollusks, there are few veins or capillaries. The place of these vessels is taken by an extensive and all pervasive system of blood sinuses. Sooner or later, the blood which has been poured from the arteries into the various

sinuses finds its way back to the large HÆMOCŒLE, or PERICARDIAL SINUS, in which lies the heart. The latter is not a vestige of the cœlom, as in the mollusks, but is a specialized part of the blood-sinus system. When the heart expands, the blood occupying the hæmocœle enters through ostia in its sides; and when the heart contracts, the blood, controlled by means of valves, is forced out into the arteries, and thence all over the body.

h. Other Organs and Systems.—The respiratory organs of the arthropods are gills (BRANCHIÆ) in the Crustacea; GILL BOOKS, LUNG BOOKS, or TRACHEÆ (air tubes) in the Arachnida; and TRACHEÆ in the Myriapoda and Hexapoda (insects). Gills are usually leaflike or feathery outgrowths of the body wall that are well provided with blood sinuses and have very thin walls. Gill books and lung books, as the names imply, consist of closely packed sheets of the body surface bound together like the leaves of a book. They may be either exposed on the surface to the surrounding water, as in Limulus; or they may be inclosed in pockets but exposed to indrawn air currents, as in the scorpions and spiders.

The EXCRETORY ORGANS of arthropods are highly variable in different groups. In the Onychophora they are segmentally arranged annelidlike nephridia, in some Crustacea they occur as a single pair of green glands, and several other kinds of excretory organs characterize other groups.

B. Representative Arthropoda

In this place it is proposed merely to present a brief synopsis of the arthropod groups with characterizations of and illustrations of a few representative types. The phylum we are surveying is so immense in numbers and so diversified in structure and habitat that we are able to indicate its range only by the method of sampling.

It is customary to divide the Phylum Arthropoda into two major sections on the basis of whether they are aquatic or terrestrial in their respiratory adaptations. Whether this is a valid criterion of affinities is an open question; at least it furnishes a convenient basis for classification. These two sections are: *a*, BRANCHIATA (breathing by means of gills or branchiæ), including but one class, Crustacea; *b*, TRACHEATA (breathing by means of tracheæ or equivalent air breathing organs), including the classes Onychophora, Myriapoda, Insecta, and Arachnida. These five classes

will be dealt with in the order mentioned. In recent years specialists in the study of arthropods have divided the phylum into eight classes, but for the sake of simplicity we shall adhere to the traditional four classes.

Class I. Crustacea.—This class is primarily aquatic in habitat, though there are not a few terrestrial or semiterrestrial repre-

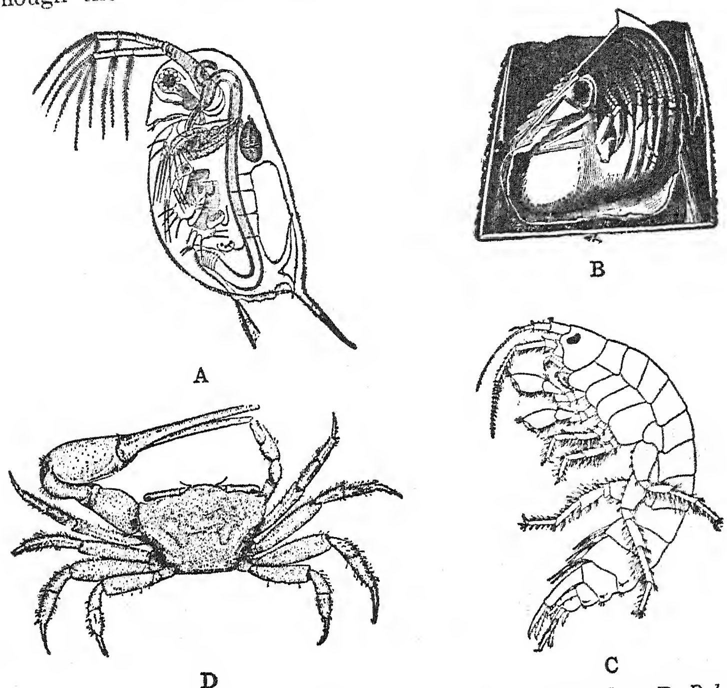


FIG. 160. Representative Crustacea. A, *Daphnia*, a water-flea. B, *Balanus tintinnabulum*, a barnacle, with one-half of shell removed to show the animal itself. C, *Gammarus fasciatus*, a fresh-water amphipod. D, *Gelasimus minax*, fiddler or soldier crab. (A, from Parker and Haswell; B, from Sedgwick, after Claus; C, D, from Paulmier.)

sentatives. Whether they live in water or on land they all breathe with gills. The body is composed of three divisions, the head, the thorax, the abdomen. Sometimes thorax and head are fused into a cephalothorax. The six-segmented head bears five pairs of appendages: two pairs of antennæ, one pair of mandibles, and two pairs of maxillæ. The rest of the body bears a highly variable assortment of appendages, differing in number, form, and function.

Five subclasses of Crustacea are distinguished:—

Subclass 1. Branchiopoda.—This is believed to be the most primitive group of modern Arthropoda. In general, there is less specialization of the body regions and their appendages than in any other group. A very common type of this subclass is Daphnia, a water flea (Fig. 160, A), which though primitive in some ways is highly specialized in others. Daphnia occurs in enormous numbers in our lakes and streams. It has been estimated that in one cubic meter of lake water in some regions there are 40,000 specimens of Daphnia and other small crustaceans. These tiny forms furnish an indispensable food supply for young fishes and other small fry.

Subclass 2. Ostracoda.—They are characterized by having the body very short and laterally compressed, covered by a bivalve shell. This group is more abundant in the sea than in fresh waters, but such copepods as Cyclops are common in fresh-water ponds.

Subclass 3. Copepoda.—This group plays about the same rôle in the oceans as do the two previous subclasses in the fresh waters. These tiny forms lack a covering shell and have no appendages on the abdomen except on the terminal segment.

Subclass 4. Cirripedia.—This is a group of degenerate sessile crustaceans, some of them being intensely parasitic. The barnacles (Fig. 160, B) are the typical representatives of the group and are characterized by being fixed during the adult period upon rocks, piles, or ship bottoms. The body is entirely inclosed in a shell that often has the consistency and appearance of a somewhat complex mollusk shell. The head parts of the animal are almost entirely wanting and the appendages are used merely in creating a current for purposes of food gathering. Sacculina, a parasitic cirripede, is discussed in detail in another connection (pp. 532, 533) and its life history is shown in Figure 262.

Subclass 5. Malacostraca.—This division includes all of the higher crustacea, such as crayfishes, lobsters, crabs, shrimps, amphipods, isopods. There are at least ten orders of Malacostraca, some familiar, such as the three discussed below, others relatively little known to the layman.

The Order *Isopoda* consists of a vast assemblage of medium-sized marine, fresh-water, and land crustaceans. Some are parasitic and very degenerate. The sow bug, Oniscus, and the pill bug,

Armadillium, are familiar isopods found under logs, stones, or boards, and are generally thought of by the layman as insects. These terrestrial crustaceans breathe by means of abdominal gills and are confined to moist places.

The Order *Amphipoda* comprises many species of marine and a few species of terrestrial crustaceans, such as sand hoppers or beach fleas. The so-called fresh-water shrimp, Gammarus (Fig. 160, **C**), is one of the best known of the amphipods.

The Order *Decapoda* contains most of the large crustaceans that are of economic importance because of their food value. The lobsters are the most valuable; crabs come next; and shrimps are not far behind. An interesting example of the most highly specialized group of this order is the sprightly fiddler crab, Gelasimus (Fig. 160, **D**).

Class II. Onychophora.—Although some authors place these animals within the class Myriapoda, there is good reason for granting them class value. It is a concise and compact assemblage of over seventy species belonging to ten genera, the best known being Peripatus (Fig. 161, **A**). These are very widely distributed over the world, but their range is extremely interrupted, for they are present in Africa, Australia, New Zealand, Tasmania, South and Central America, Mexico, West Indies, and Malaya. The most interesting point about Peripatus is that it is a classic connecting-link type, having characters of the Phylum Annelida and of the Phylum Arthropoda; and thus the group tends to prove what is generally believed on other grounds, that the arthropods have had an annelidan ancestry. The annelid features of Peripatus are: annelid-like nephridia segmentally arranged; cilia in reproductive organs; general annelid arrangement of the chief systems. The arthropod characters are: the cœlom is filled with blood and blood sinuses; appendages are somewhat jointed and some are modified as mouth parts; tracheæ are present.

Class III. Myriapoda.—These are the centipedes and millipedes. They are characteristically elongated forms, with a distinct head possessing one pair of antennæ and one pair of mandibles, and with a multiplicity of more or less insect-like paired appendages showing little regional specialization. There are four orders, which some authorities have elevated to the status of classes.

The Order *Diplopoda* comprises such typical millipedes as that shown in Figure 161, **B**. These commonly have a cylindrical body

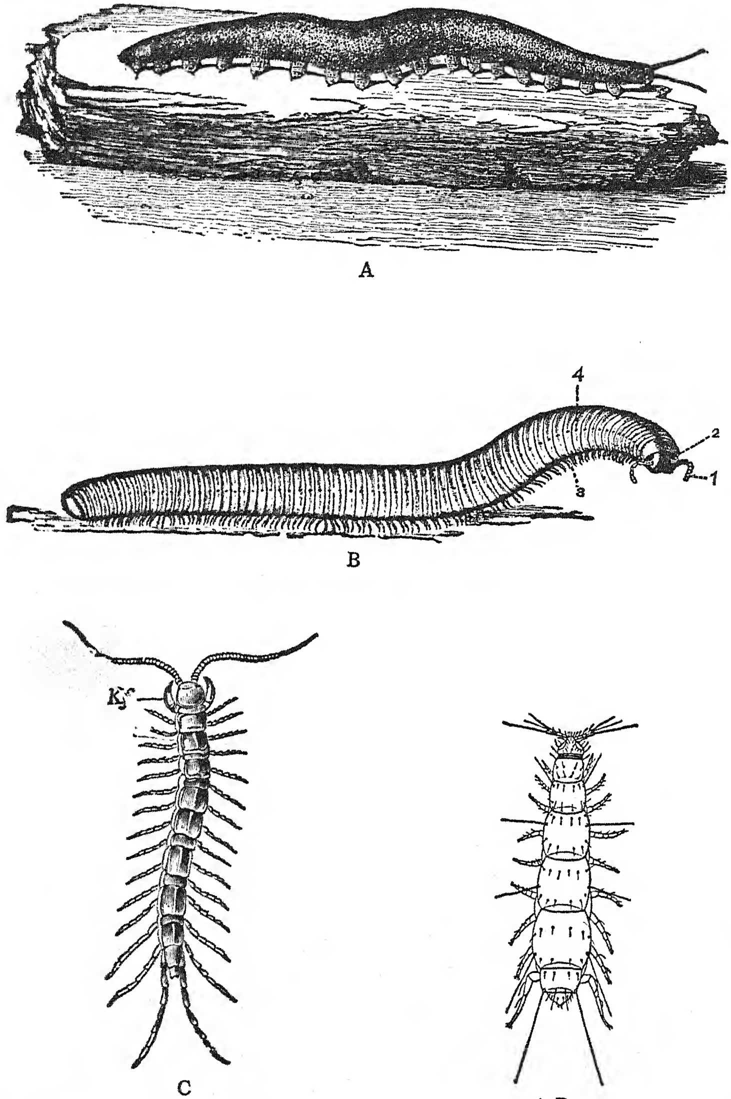


FIG. 161. Representative Myriapoda and Onychophora. A, *Peripatus capensis*, an arthropod with several annelid characters. B, a millipede; C, a centipede, *Lithobius forficatus*. D, *Pauropodus huxleyi*, a centipede with only nine pairs of legs, and having the general appearance of an insect. (A, from Sedgwick; B, from Shipley and MacBride, after Koch; C, from Sedgwick, after Koch; D, from Sedgwick, after Latzel.)

covered with chitinous armor, and they have the habit of rolling up into a close spiral when disturbed.

The Order *Chilopoda* consists of the more typical centipedes such as Lithobius (Fig. 161, C). They are dorsoventrally flattened and have longer though fewer appendages than the Diplopoda.

The Order *Pauropoda* (Fig. 161, D) comprises very minute degenerate myriapods, with relatively few appendages.

The Order *Symphyla* consists of small myriapods with twelve pairs of appendages. They are interesting mainly on account of the fact that they resemble certain of the more primitive wingless insects in general appearance and in habits. This suggests that the insects may have arisen from some now extinct myriapod stock.

Class IV. Insecta.—The following classification of insects recognizes twenty-four orders. These orders may be distinguished from one another mainly on the basis of their differences with respect to three characteristics: *a*, the presence or absence of wings, or the form of the wings; *b*, the structure and function of the mouth parts; *c*, the relative completeness or incompleteness of the metamorphosis.

Entomologists are not fully in agreement as to the classification of insects, but American specialists mostly agree on the following twenty-four orders:

Order 1, *Thysanura* . . .	Bristletails, fish-moths, etc.
Order 2, *Collembola* . . .	Springtails.
Order 3, *Orthoptera* . . .	Cockroaches, grasshoppers, locusts and crickets, etc.
Order 4, *Isoptera*	Termites (white ants).
Order 5, *Neuroptera* . . .	Ant-lions, aphis-lions, the Dobson, etc.
Order 6, *Ephemerida* . . .	Mayflies.
Order 7, *Odonata*	Dragonflies.
Order 8, *Plecoptera* . . .	Stoneflies.
Order 9, *Corrodentia* . . .	Book-lice, bark-lice, etc.
Order 10, *Mallophaga* . . .	Bird-lice.
Order 11, *Embiidina* . . .	Embiids.
Order 12, *Thysanoptera* . .	Thrips.
Order 13, *Anoplura* . . .	Sucking lice.
Order 14, *Hemiptera* . . .	True bugs.
Order 15, *Homoptera* . . .	Plant-lice, scale-insects, etc.

Order 16, *Dermaptera*	Earwigs.
Order 17, *Coleoptera*	Beetles.
Order 18, *Strepsiptera*	Stylopids.
Order 19, *Mecoptera*	Scorpion-flies, etc.
Order 20, *Trichoptera*	Caddice-flies.
Order 21, *Lepidoptera*	Moths, skippers, butterflies.
Order 22, *Diptera*	Flies, gnats, mosquitos, etc.
Order 23, *Siphonaptera* . .	Fleas.
Order 24, *Hymenoptera* . .	Bees, wasps, ants, etc.

Of these orders the best known and most important economically and in other ways are Orders 3, 4, 7, 14, 15, 17, 21, 22, and 24. All of these orders are vast assemblages of successful and highly diversified species. The ending "ptera" of many of these names means wings.

The Order *Orthoptera* consists of some of the most numerous and destructive species, whose ravages upon crops are proverbial as far back as history goes. A relatively harmless representative of the order is the rather attractive katydid (Fig. 162, *A*).

The Order *Isoptera*, commonly called "white ants" though they are not ants at all, are especially interesting because of their elaborate social organization. They are also important economically because of their wood eating habits.

The Order *Odonata*, though not so abundant as some orders, and of no great economic importance, is among the most interesting of insect orders because of the large size, conspicuous form, curious predaceous habits both of larvæ and of adults, and their remarkably abrupt metamorphosis. The dragon fly, Libellula (Fig. 162, *B*), is a good example of the order.

The *Hemiptera* are numerous and of great economic importance. The common chinch-bug is at once one of the best known and the most dreaded of agricultural pests (Fig. 162, *D*).

The Order *Homoptera* is well known because the aphids and scale insects do so much damage to cultivated plants.

The *Lepidoptera* are perhaps the most attractive as well as the most destructive of insects. The butterflies and moths do their chief damage in the caterpillar, or larval, state. After metamorphosis into the "angel form" they behave in a way that is appropriate to the angel state, feeding chiefly upon the nectar of flowers and doing no harm. The cabbage butterfly, *Pieris rapæ* (Fig. 162, *C*), is one of the commonest of butterflies in the world.

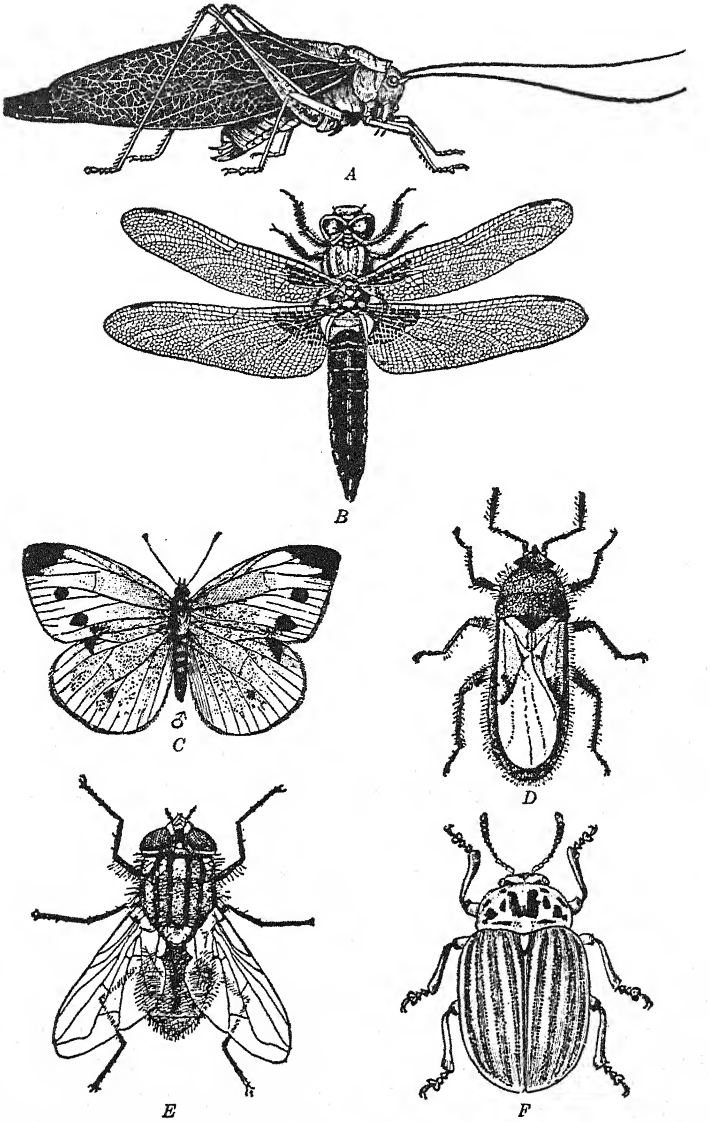


Fig. 162. Representative Insecta. *A*, katydid, *Microcentrum retinerve*. *B*, a dragon-fly, *Libellula depressa*. *C*, cabbage butterfly, *Pieris rapæ*. *D*, chinch-bug, *Blissus leucopterus*. *E*, house-fly, *Musca domestica*. *F*, potato-beetle, *Leptinotarsa decemlineata*. (*A*, from Sedgwick, after Riley; *B*, from Miall, after Charpentier; *C*, after Webster; *D*, from Osborn, after Riley; *E*, from Howard; *F*, from the Cambridge Natural History.)

The *Diptera* might receive the distinction of being pests *par excellence.* If man could select one order of animals to be rid of he would do well to select the Diptera. Think what a relative paradise the world might be without the flies, mosquitoes, gnats, and all that pesky tribe. Moreover, we would incidentally get rid of many of our worst insect transmitted diseases, as is borne out in Chapter XXVIII. Of all the flies the most familiar is *Musca domestica*, our constant household companion (Fig. 162, *E*).

The *Coleoptera* (beetles) are among the largest and most successful of the insect orders. While less annoying to man's person and health than the Diptera, they are far more destructive of his crops and other property. One need only mention in this connection one example, the Colorado potato beetle (Fig. 162, *F*).

The *Hymenoptera* are the most important from almost any point of view of the insect orders. They represent a truly dominant group. Little need be said here about the ants, bees, and wasps, for they are made the subject of special discussion in Chapter XXVII.

Class V. Arachnida.—This large and diversified group includes the king crabs, the scorpions, the spiders, the harvestmen, the ticks, the mites, and several less familiar orders. They are characterized by the absence of antennæ, the absence of true jaws, and the division of the body into three regions (prosoma, mesosoma, and metasoma). All but the king crabs are fundamentally terrestrial and breathe by means of lung-books or tracheæ. Of the eleven orders we need mention only four.

The Order *Xiphosura* (king crabs) constitutes an interesting relic of the very remote past that has come on through the ages little changed from the ancestral state. The genus Limulus (Fig. 163, A) consists of large marine arachnids, with a tough horseshoe-shaped carapace covering the body so completely that they seem to be immune to almost any attack. They possess large numbers of sheetlike branchiæ bound together like the leaves of a book, and hence called gill-books.

The Order *Scorpionida* are predaceous arachnids that may reach a considerable size and are noted for their poison sting on the end of the whiplike tail, or metasoma, by means of which they paralyze their prey and protect themselves from their enemies. Their mating behavior is especially interesting and curious. After some strange antics while facing each other, the male seizes the chelæ of the female and the two engage in a curious formal dance or, as

Fabre calls it, a *promenade à deux* (Fig. 163, C), after which mating ensues.

The Order *Araneida* consists of the spiders, a highly specialized and fascinating group from the naturalistic standpoint. They are especially noteworthy because of their spinning habits and

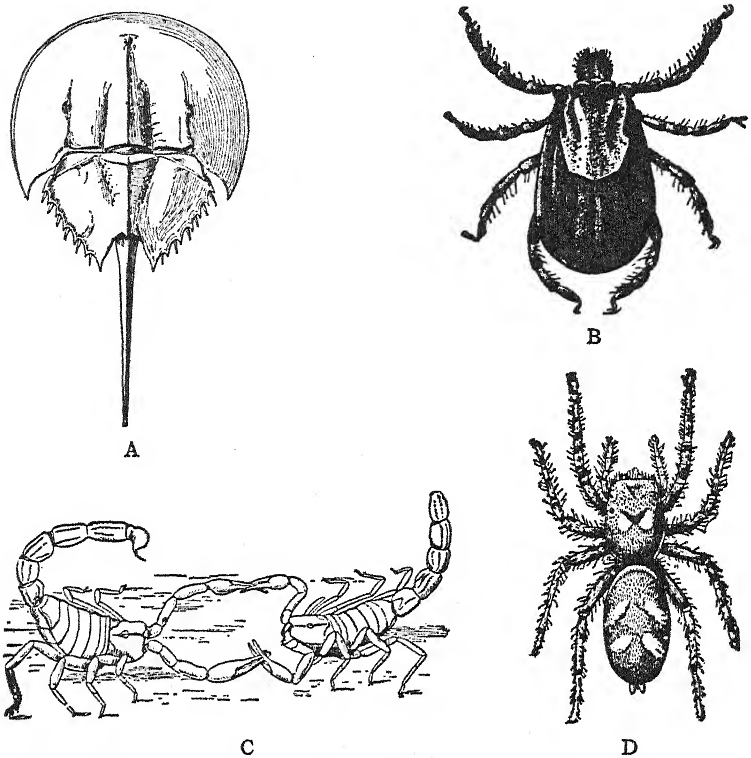


FIG. 163. Representative Arachnida. A, dorsal view of the King crab, *Limulus*, a marine arachnid. B, cattle tick, *Boöphilus annulatus*. C, a pair of scorpions (*Buthus occitans*) engaged in the "*promenade à deux*" or mating act. D, jumping spider, *Attus*. (A, from Shipley and MacBride; B, after Packard; C, after Fabre; D, from Davenport, after Emerton.)

their poison fangs. They construct snares of the most elaborate architecture for capturing prey and also use their silky threads for the construction of all sorts of shelters and abodes, as well as cocoons for the protection of their eggs and young. They show very little external evidence of their segmental structure, have eight

walking legs, and usually many small eyes, which give them clear vision only at very short range. Among the liveliest of the spiders are the jumping spiders, one of which is shown in Figure 163, **D**.

The Order *Acarina* consists of the ticks and mites, an immense assemblage of rather small forms, many of them characterized by their ectoparasitic habits. Some of them merely suck the blood of the host, others burrow beneath the skin and cause severe irritation. Perhaps they are most significant on account of their propensity for transmitting diseases from one host to another. The cattle tick (Fig. 163, **B**) is responsible for the dreaded Texas fever, the loss from which runs up to about $100,000,000 a year in the United States. The majority of mites are free living, occurring in leaf mold, under stones, and in water.

In our further discussion of this large and important phylum our plan is to deal with a number of typical representatives of the group in such a way that each will serve to illustrate some important biological phenomenon or principle. Thus, when discussing the crayfish, we shall emphasize chiefly the principle of homology, especially that of serial homology; in dealing with grasshoppers, emphasis is laid on crop damage done by these insects and methods of control; in dealing with ants, our chief aim is to give the facts about communal life in this most interesting group and to develop some of its implications; while flies, mosquitoes, fleas, are dealt with chiefly as agents in the transmittal of disease. In the subsequent chapter dealing with adaptations a good many other interesting facts about arthropods are given. It has been our purpose in this place merely to outline the chief characteristics of the phylum.

SUMMARY

1. The Phylum Arthropoda is the largest of all phyla in numbers of species, over half a million having been described.

2. Arthropods have the same type of axiate organization as annelids.

3. Arthropods also resemble annelids in the method of cœlom formation; metameric organization; cerebral ganglia connected around the œsophagus by commissures with the solid, paired ventral nerve cords.

4. Arthropods differ from annelids as follows: jointed appendages; limited number of segments; greater specialization of metameres; greater cephalization, head composed of six segments; open circulatory system; cœlom displaced by a system of blood sinuses, chief of which is the hæmocœle surrounding the heart; a definite exoskeleton; no trochophore larva.

5. The members of the Class Crustacea are largely aquatic. They are characterized by having two pairs of antennæ; gills; body usually divided into head, thorax and abdomen, though head and thorax may be fused.

6. The Class Onychophora, with its famous genus Peripatus, constitutes a connecting link between annelids and arthropods, for it possesses a combination of the characteristics of the two phyla.

7. The members of the Class Myriapoda are terrestrial arthropods with tracheæ, large numbers of walking legs, one pair of antennæ, a well-defined head, but no division of trunk into thorax and abdomen. They appear to have close affinities with the insects.

8. The Class Insecta is the most successful of all invertebrate groups. Insects have one pair of antennæ; a division of the body into head, thorax, and abdomen; tracheæ; no more than six legs; usually wings in adults; true jaws.

9. The Class Arachnida, consisting of king crabs, scorpions, spiders, ticks, and mites, is characterized by lack of antennæ; usually eight legs; head fused with thorax; breathe with lung-books, gill-books, and tracheæ; no true jaws, the nippers or fangs (cheliceræ) being the first pair of appendages.

CHAPTER XXV

THE CRAYFISH AND THE PRINCIPLE OF SERIAL HOMOLOGY

(PHYLUM ARTHROPODA)

Crayfishes of the genus Cambarus are favorite laboratory types, and are here introduced especially to illustrate the important principle of Serial Homology. A short account of their activities and of their habitat, together with a brief consideration of their general morphology, precedes the discussion of the main point at issue.

A. Habits and Habitat

Crayfishes have often been called fresh-water lobsters because of their close resemblance to the latter and because they are believed to have been derived as an offshoot from the lobster tribe. One usually finds crayfishes hiding under stones or other cover during the day, but they are quite active at night. Their habit is to lie in wait behind shelters and to dart out upon unwary fishes or insects that pass within their reach, seizing them with their powerful pinchers (chelipeds) and rending them to pieces. Though preferring living animal food they are not averse to dead and decaying flesh, and they even resort to plant food in times of food scarcity. The crayfish is well protected, owing to the fact that its color closely matches that of the background, making it inconspicuous both to prey and to enemies. Its characteristic backward method of locomotion is especially well-adapted for avoiding enemies.

B. General Morphology

The crayfishes belong to the Phylum Arthropoda and the Class Crustacea. Like the annelids, the arthropods are metameric, but they exhibit a rather profound modification of the primitive segmental plan. Externally, the evidences of segmentation are quite obvious in connection with the exoskeletal rings and in the paired appendages (Fig. 164). Internally, however,

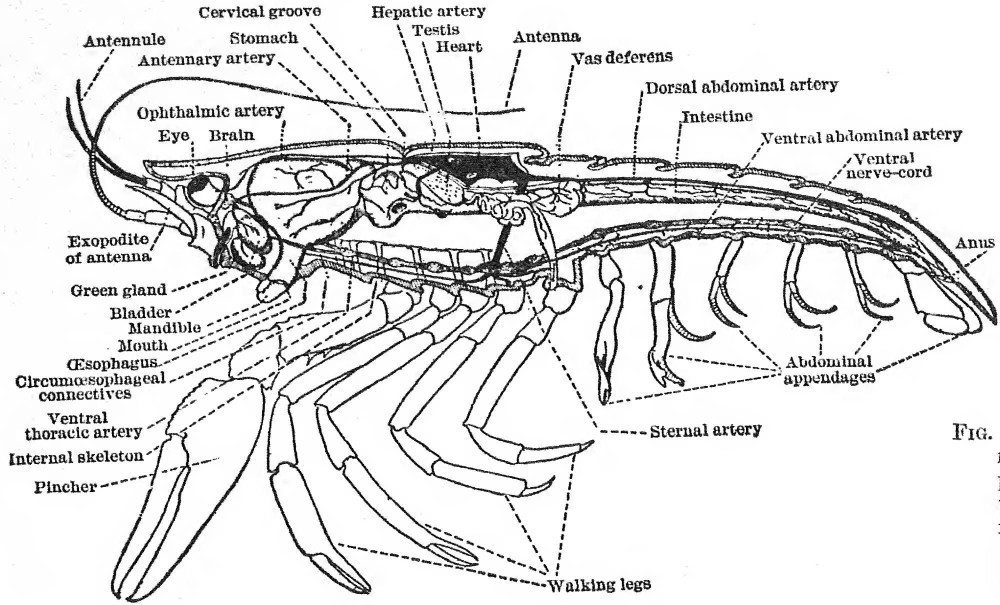


FIG. 164. Semidiagrammatic view of appendages and of internal organs of a male crayfish. (From Shipley and MacBride.)

one sees only rather vague indications of metamerism, for there are no septa dividing the cœlom into compartments, no series of paired nephridia and gonads, no obvious segmental arrangement of blood vessels or alimentary organs. The nervous system is, of all the internal systems, the most strikingly metameric; it consists of a series of paired segmental ganglia connected by paired nerve cords—an arrangement not unlike that of the annelids. The crayfish, like other arthropods, has no open cœlom, but the spaces between the viscera and the body wall are filled up with BLOOD SINUSES. The body and the appendages are covered with a tough chitinous CUTICLE, which in some regions is thick and impregnated with calcium salts. In the abdominal region each metamere is covered with a distinct ring of chitin, but the rings of the head and those of the thorax are all fused into one solid mass of armor, the CEPHALOTHORAX, which has two lateral flaps that serve as a covering for the gills, the space between them and the body forming BRANCHIAL CHAMBERS. The other systems of organs are in no essential respects greatly different from those previously dealt with.

C. Appendages and Serial Homology

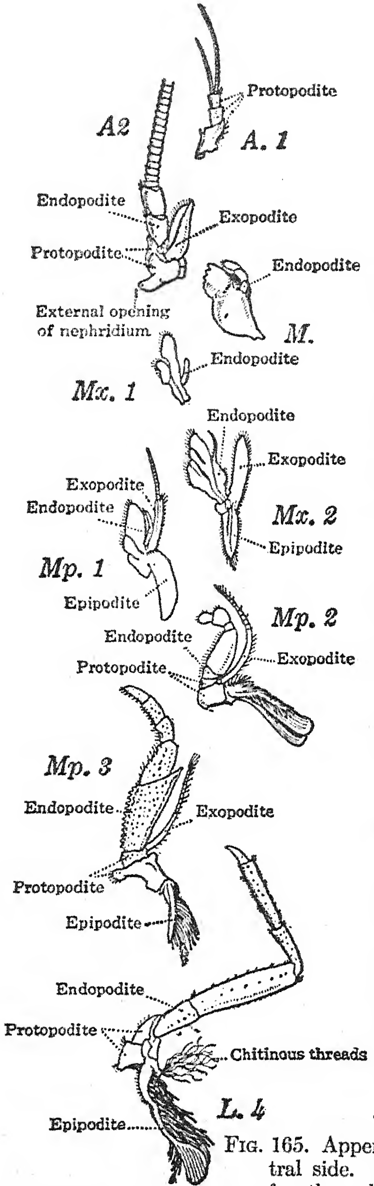
It has already been pointed out that the metameric organization of the crayfish is indicated most clearly by the appendages. ***There is a pair of appendages of some sort to each somite, or metamere.*** In the regions of the body where the somites have retained their primitive free segmental character the appendages are also found in a relatively generalized condition; but in the regions where the somites are firmly fused and closely packed together the appendages are the only external parts that give a clue as to the number of metameres represented. In these packed regions of the head and in the anterior somites of the thorax the appendages are variously specialized for different functions. All told, there are 19 (or 20) pairs of appendages: 5 (or 6) in the head, 8 in the thorax, and 6 in the abdomen. There is some divergence of opinion as to whether the stalked eyes, the first appendages of the head, are to be counted as true appendages, homologous with others. The prevailing opinion seems to be that the eyes are not strictly homologous with the other appendages, but are special appendages of the prostomium. If, however, an eyestalk is removed, an antenna-like appendage sometimes regenerates from the eye-stalk stump. This seems to suggest that the eyes are true appendages. Counting

the eyes, there are 20 pairs of appendages, which are distributed as follows:—

Head	Stalked eyes	sensory
	Antennules	
	Antennæ	
	Mandibles	feeding
	First maxillæ	
	Second maxillæ	
Thorax	First maxillipeds	feeding
	Second maxillipeds	
	Third maxillipeds	
	Chelipeds (grasping and defensive)	
	First ambulatory	walking
	Second ambulatory	
	Third ambulatory	
	Fourth ambulatory	
Abdomen	First swimmerets (much reduced in female; in male modified as copulatory organs)	
	Second swimmerets (typical in female; copulatory in male)	
	Third swimmerets	generalized function in male, egg carriers in female
	Fourth swimmerets	
	Fifth swimmerets	
	Caudal appendages (swimming)	

The SWIMMERETS, especially those of the female, are considered as the least specialized of the appendages, belonging as they do to the most generalized of the body somites. Each appendage is made up of three fundamental parts: the basal part, which is attached to the body, is called the PROTOPODITE; the two distal parts are named according to their position with reference to the median line of the body, the inner one being called the ENDOPODITE, the outer, the EXOPODITE (Fig. 165). In the first abdominal appendages of the male, the copulatory organs, the exopodites are lost, while the two remaining parts unite to act as a sort of semitubular channel for the transfer of sperm into the annulus, or seminal receptacle, of the female. The last abdominal appendages have all three parts present in a broadly expanded condition so that they furnish the chief paddle surface for backward swimming.

All of the WALKING APPENDAGES have lost the exopodites and



consist mainly of the enlarged, many-jointed endopodite, which may or may not end in pincers. The protopodite gives off from its base a GILL and a membranous EPIPODITE, or BRACT, which serves to close off the gill chamber from the outside. A CHELIPED is merely an enlarged ambulatory organ with its terminal joint enormously overgrown into a powerful CHELA, or claw. The pairs of MAXILLIPEDS differ each from the others. The THIRD MAXILLIPED resembles a walking leg, but has a small gill and an antennalike exopodite. The SECOND MAXILLIPED has a much reduced endopodite, an antennalike exopodite, a rudimentary gill, with a well-developed bract. The FIRST MAXILLIPED has both exopodite and endopodite much reduced, no gills, and relatively large protopodite with large bract.

In the head the first appendages are the STALKED EYES, which probably represent the protopodite alone. In the ANTENNULES the protopodite consists of three segments and both exopodite and endopodite are present as many-jointed filaments. In the MANDIBLES there is no exopodite, the jaw proper

FIG. 165. Appendages of Crayfish as seen from ventral side. *A. 1,* antennules; *A. 2,* antennæ; *L. 4,* fourth walking leg; *M.,* mandible; *Mp. 1,* first maxilliped; *Mp. 2,* second maxilliped; *Mp. 3,* third maxilliped; *Mx. 1,* first maxilla; *Mx. 2,* second maxilla. (From Kerr.)

being the modified protopodite, while the endopodite is present as a small jointed palp. In the FIRST MAXILLÆ the exopodite is wanting, but in the SECOND MAXILLÆ all three parts are represented.

All of these appendages, with the possible exception of the eyes, have equivalent embryonic rudiments and, at an early stage, appear to be essentially alike. As they grow, they modify in different ways and come to subserve a great variety of functions, some being only sensory, others only ambulatory, others gustatory, copulatory, or swimming. Some play a mixed rôle, as has already been shown. In the process of specialization from the generalized embryonic type some parts start to grow, then cease, and either become resorbed or remain as vestiges. We have here a fine example of the specialization of similar structures for different functions. ***Organs that have a similar embryonic origin and similar morphological relations are said to be homologous,*** and those that are homologous, but in different metameres of the same animal, are termed ***serially homologous.*** These structures, specialized as they are for different functions, are classed as ***adaptations.*** One of the greatest of our unsolved biological problems is to account for the origin of adaptations. A consideration of this problem will be found in Chapter XLIX.

While we cannot take the time to deal in any detail with homologies that exist between structures of the crayfish and those of other Crustacea, we must at least indicate some of the facts. We find that one whole group of Crustacea, the Malacostraca, has the same number of appendages as has the crayfish, five (or six) in the head, eight in the thorax, and six in the abdomen. But beyond this there is considerable diversity. In one group only three of the thoracic appendages are used for walking, the rest being employed in feeding; in another group all eight thoracic appendages are in a rudimentary state; in still another group seven thoracic appendages are ambulatory and only one is used in feeding.

The general conclusion that is usually drawn from these facts is that all of these different types of Crustacea, because of their fundamental similarities, must be more or less closely related, and must have descended from common ancestors. Today homologies are interpreted as among the most reliable evidences of the blood relationship of diverse groups and, indirectly, of descent with modification.

SUMMARY

1. When two structures in different metameres are similar in embryonic origin and have the same anatomic relations they are said to be serially homologous even though they are different in appearance and in function.

2. The nineteen (or twenty) pairs of appendages in the crayfish well illustrate the principle of serial homology.

3. The typical crustacean appendage is biramous, having one basal joint (protopodite), which divides distally into two terminal parts (exopodite and endopodite). The exopodite is wanting in many of the more specialized appendages.

CHAPTER XXVI

THE NATURAL HISTORY OF THE GRASSHOPPER

(PHYLUM ARTHROPODA)

A. Habits and Habitat

1. *Introduction*

In choosing one out of many thousands of kinds of insects for especial attention we are not guided by favoritism. Personally, the writer would rather consider the butterfly or the bee, were physical attractiveness to guide his choice. There are reasons for selecting the quaint and ubiquitous grasshopper. It is a representative insect, not too primitive nor yet too specialized; it is of convenient size for laboratory work; it is extremely widespread and abundant; and it is of unusual economic importance.

There are many kinds of grasshoppers (Fig. 166). Some kinds are called locusts, but there is no well-defined scientific distinction between locusts and grasshoppers. Our account of grasshopper natural history will not confine itself to any one species, but will serve as a representative account for a considerable group of similar forms.

The grasshopper, using the term broadly, is a typical representative of the insect order Orthoptera, which includes crickets, katydids, cockroaches, walkingstick insects, and some other less familiar forms. They are characterized by having biting, or mandibulate, mouth parts; two pairs of wings, the anterior pair usually somewhat thickened; incomplete metamorphosis, a type of development in which the transition from larva to adult is through several larval stages and not all at once.

2. *Habitat and Distribution*

As the name indicates, grasshoppers are grass dwellers in the broad sense, in that they inhabit mainly meadows. Some species prefer the dry, dusty fields; other species prefer damp, lush meadows and lowlands. Wherever you may go about the open fields of the

world, there you will find grasshoppers. Some species have a very narrow range, others have a continent-wide distribution. Some forms have a migratory habit, swarming over hundreds of miles of territory in countless hordes, eating up all green vegetation in their path, leaving desolation in their wake.

The warrior grasshopper, *Camnula pellucida,* is one of the most serious insect pests of the Middle Western states. They are re-

A

B

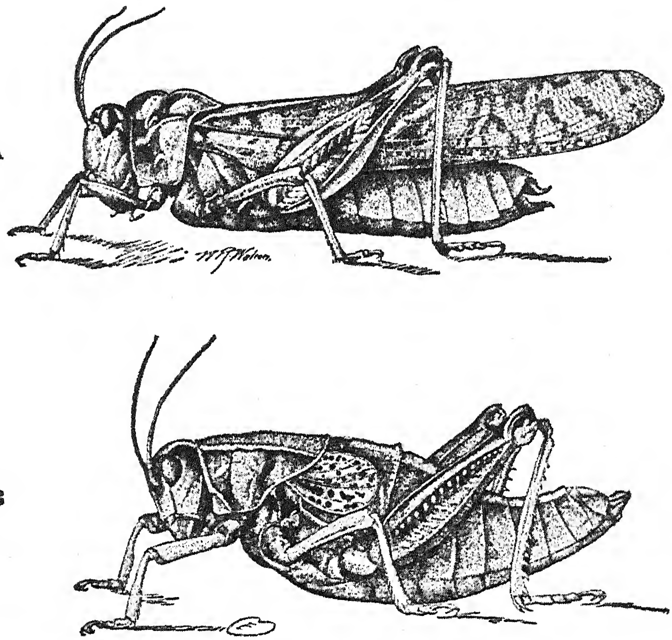


FIG. 166. Typical Locusts (Grasshoppers). A, *Dissosteira longipennis;* B, *Brachystola magna.* Both females. (From Farmers' Bulletin, No. 747, U. S. Dept. Agric.)

sponsible for "plagues" which are doubtless of the same sort as the biblical "plague of locusts" that tormented the Egyptians. In a plague year, owing to relative lack of enemies or favorable developmental conditions, a large percentage of the eggs laid develop and hatch. They hatch in May or June, and in the course of a few hours enormous numbers emerge and begin to migrate. They jump and crawl toward the sun. At this stage they have no wings and cannot fly. Since in most regions the rains come mainly in

the afternoon, the grasshoppers follow the morning sun and hence move mainly in a southeasterly direction. When an army of these insects crosses a cultivated field they denude it of all green vegetation, leaving it utterly desolate. After the last larval molt the wings are ready for flight and the migration is then sometimes carried on through the air, dense clouds of grasshoppers traveling *en masse* and dropping down upon the cultivated fields.

3. *Control of Grasshoppers*

There are various kinds of natural checks upon the overproduction of grasshoppers. The eggs are easily killed in the ground during the winter if exposed to frequent freezing and thawing. Enormous numbers are killed off at various stages by insect and other enemies. Grasshopper eggs are relished as food by various types of ground-burrowing animals, such as field mice, gophers, and moles; while the young and adults are devoured in enormous numbers by birds, lizards, and skunks. Even the despised snakes of our fields take heavy toll of grasshopper life and thereby help to justify their existence in a world turned against them.

Among the insect enemies of grasshoppers are other insects that lay their eggs among grasshopper eggs, so that their young larvæ may feed upon the handy larvæ of their prey. Even plants may be parasitic on grasshoppers, as is evidenced by the large numbers found dead of a fungus disease.

Internal parasites of various sorts, including worms and bacteria, are ever present, as in all other animals, and help in the destruction of grasshoppers. Thus there is a continual conflict between the tremendous forces of reproduction and the complex forces of destruction. The result is that under ordinary conditions the various species are kept down to reasonable numbers. Under exceptionally favorable conditions the forces of reproduction gain the ascendancy and we have a "plague year." Greater success of the grasshopper increases the number of parasites and other enemies and the next year the species is back to normal or below it.

No better example could well be cited to illustrate the idea of the "Web of Life" by which is meant that no species lives to itself alone, but exists in the midst of a whole community of interdependent species. There is thus a balance in nature that is self-regulatory. This is an ecological consideration of the highest significance.

B. Physiology of the Grasshopper

1. *Feeding Habits and Digestion*

In feeding, the grasshopper nips off with the mandibles small bits of grass or leaves. The LABRUM is used as an upper lip and the LABIUM as a lower lip. These act as aids in food ingestion and as tactile organs. Glands of the mouth secrete a SALIVARY JUICE that helps to lubricate the food and probably serves as a digestive fluid that acts upon the food after it reaches the CROP, an enlarged region of the alimentary tract used primarily for storage. The food passes from the crop into the STOMACH, composed of a PROVENTRICULUS and a VENTRICULUS, where the main digestive changes occur. The GASTRIC CÆCÆ pour their abundant juices into the stomach. It is this material, colloquially called "molasses" or "tobacco juice," that exudes from the mouth of a grasshopper when caught and handled. The process of digestion continues in the intestine and absorption of the diffusible products of digestion takes place in this region.

2. *Sense Organs in Relation to Behavior*

The principal senses of the grasshopper are the same as in most other animals: touch, taste, smell, hearing, and vision. The SENSE OF TOUCH is rather generally distributed over the body, but especially centered in the antennæ, mouth parts, and abdominal cerci. The SENSE OF TASTE is largely confined to the median portion of the labium. The SENSE OF SMELL appears to be situated in the basal portions of the antennæ. The SENSE ORGANS OF HEARING are the so-called TYMPANIC MEMBRANES, situated on the sides of the abdomen on the first abdominal somite. These organs are believed to have a most important relation to the sound-producing STRIDULATION APPARATUS so characteristic of the grasshoppers and their allies. In some of the grasshoppers the sound is produced by rasping the hind legs across the hard anterior wings, or by rubbing the wings and wing covers together in flight so as to produce the well-known "clacking" sound. In some of the allies of the grasshoppers such as the crickets and katydids, the sound is described as chirping. These sounds are sex calls and serve to guide the female to the male. The SENSE ORGANS OF SIGHT are the COMPOUND EYES and the OCELLI. An ocellus is a simple eye consisting of a transparent lens-shaped thickening of the exoskeleton with a

visual sense area beneath, which is connected with the central nervous system. Probably these eyes form only the vaguest of images and serve largely as light perceptive organs. The compound eyes are much more complex, being made up of numerous OMMATIDIA, each of which is a simple eye. The prevailing theory of the functioning of these eyes is that each visual unit sees one part of the image. The curvature of the whole eye is such that only those ommatidia perpendicular to the rays cast by a given object form a clear image. Thus when an object moves, a series of shifting images is formed. This gives the animal definite information about objects in movement in the immediate surroundings; how fast and in what direction the object is moving. Nothing could be more important than this information in the life of a creature so much preyed upon as is the grasshopper.

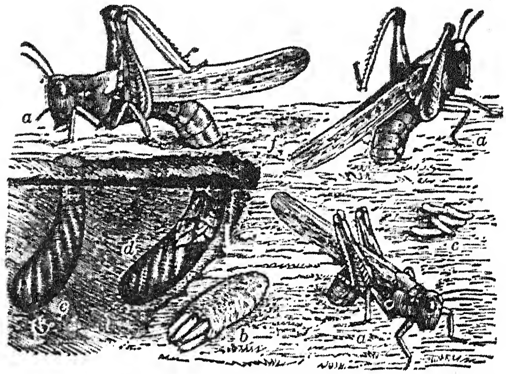


FIG. 167. Rocky mountain locust, showing *a*, *a*, *a*, females in different positions laying eggs; *b*, egg pod removed from ground; *c*, eggs lying loose on ground; *d*, and *e*, burrows in ground for deposit of eggs. (From Hegner, after Riley.)

C. Reproduction and the Life Cycle

During the mating season males and females clasp each other by means of special copulatory organs at the end of the abdomen. The eggs are fertilized internally and are then laid by the female by means of the ovipositor, an organ on the end of the abdomen that enables the latter to thrust itself some distance into the ground (Fig. 167). Masses of eggs, held together by a sticky secretion, are deposited and, when the abdomen is withdrawn, are buried beneath a layer of loose earth. In order to develop and hatch, the eggs must lie just beneath the surface. If the surface be plowed under, the eggs and embryos are killed. The embryonic development proper takes place within the egg, and the young hatches out as a small larva that looks a good deal like a grass-

hopper, except that it seems to be mostly head and has no wings. The young develops through a series of molts, each successive larval stage being more like an adult grasshopper. The last molt is followed by the adult type, technically called the IMAGO, which spends the rest of its life in this form, neither growing nor molting. Some of the larval, or nymph, stages are shown in Figure 168.

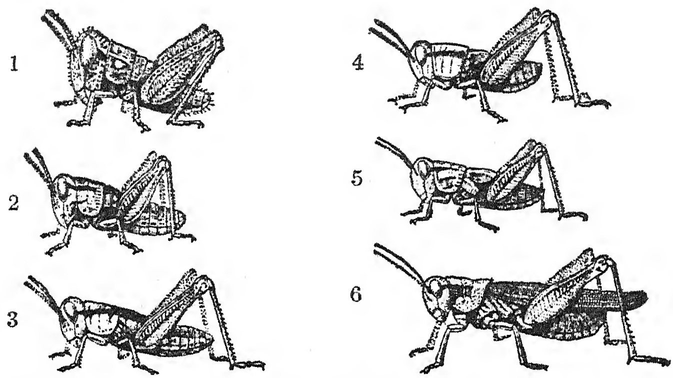


FIG. 168. Some of the stages of metamorphosis in the grasshopper. 1 to 5 are nymph stages; 6 is a young imago. (From Packard, after Emerton.)

This brief account of the natural history of the grasshopper is intended to supplement a laboratory study of its anatomy. No general account of the anatomical details is given in this place, because it is much better for the student to work them out at first hand. The points brought out here are chiefly those that cannot be brought out through a laboratory study.

SUMMARY

1. The grasshopper belongs to the Phylum Arthropoda, Class Insecta, and Order Orthoptera. It is chosen as a representative insect because it is more commonly used as a laboratory type than any other.

2. Grasshoppers are among the most important enemies of the farmer and much work has been done in attempts to control them and prevent their damaging attacks.

3. One of the most striking features of the natural history of the grasshopper is its numerous larval stages (instars). There is no pupal stage and there is no complete metamorphosis at one step, as there is in many of the higher orders.

CHAPTER XXVII

ANTS AND SOCIAL ORGANIZATION (PHYLUM ARTHROPODA)

ANTS have for a long time attracted the attention of naturalists because of their social organization. For ages they have occupied a dominant place in the economy of nature because they are so highly adapted to the conditions of life. Their success in the world is attested by their extraordinary abundance and wide distribution. Three factors, more important perhaps than any others, have made for success: their exquisite subterranean life, their polymorphism, and their social habits.

A. SUBTERRANEAN LIFE

Every one has seen ants in process of excavating their subterranean galleries. Processions of ants may be seen emerging from a hole in the ground, each individual carrying in its mandibles a grain of sand or a small lump of soil. Coöperative and incessant labor on their part results in the excavation of elaborate systems of tunnels and galleries, with here and there enlarged chambers used as nurseries and storehouses. The advantages of subterranean life are fairly obvious. It offers protection from both diurnal and seasonal changes of temperature; for the temperature a few feet below the surface remains relatively constant and rarely goes to extremes of heat or cold. It offers a retreat from the chief insectivorous animals, such as birds and reptiles. It furnishes storehouses for food that may be used to tide them over long periods of famine, drought, or cold, thus making it possible for most species of ants greatly to prolong individual life, some individuals living a decade or more. This is quite in contrast with the duration of life of most insects, in which a generation lasts for only a few months or a year.

B. POLYMORPHISM

Polymorphism is a term designating the existence of several different forms, or CASTES, of individual in a species. We speak of

the differences between the sexes as examples of sex dimorphism, but in the ants there are always at least three and frequently five or six distinctly different forms, some sexual and others functionally sexless. There are always the fertile females or queens, functional males, and workers of at least one kind, the latter zygotically female but sexually quite immature. In a number of species there is a caste called soldiers, characterized by enormous heads and mandibles (Fig. 169, **C**). The duties of the different castes are diverse and quite well-defined. Queens and males are merely and solely parents. Workers are, as the name implies, generalized laborers and do all of the necessary work of the colony. Soldiers are specialists in warfare and rapine. Figure 169 shows the differences in size and form of the six castes of one species of ant.

C. Social Life

Ant communities are somewhat like the more primitive human communities in that they are essentially family groups that hold together and coöperate for the common good. Sometimes, as we shall see later, mixed communities are formed as the result of slavery. The history of an ant colony will serve to reveal the nature of their social organization. At some season of the year, depending on the locality of the species in question, certain of the larvæ develop into functional males and females. These are winged types and tend to fly away from the nest and to rise high into the air to mate. After large numbers of them have been killed and eaten by birds a few return to earth, never to fly again, for the male dies and the female hunts for a hole in the ground where her eggs may be laid. The queen breaks off her wings and becomes much like other ants except for her larger size. The eggs hatch out as grubs, which are fed by a secretion produced by the mother. She starves herself sometimes for months while feeding her young, but as soon as these young reach the IMAGO state they take over the duty of feeding the exhausted mother. When well fed, she lays other batches of eggs that are cared for and reared by the workers. Lazy, and doing nothing but feed and lay eggs, she may live this sort of life for fifteen years. As time goes on, the colony becomes large and prosperous; the greater their population, the more extensive becomes the system of galleries. How long a given community may last is unknown, but one may assume that only

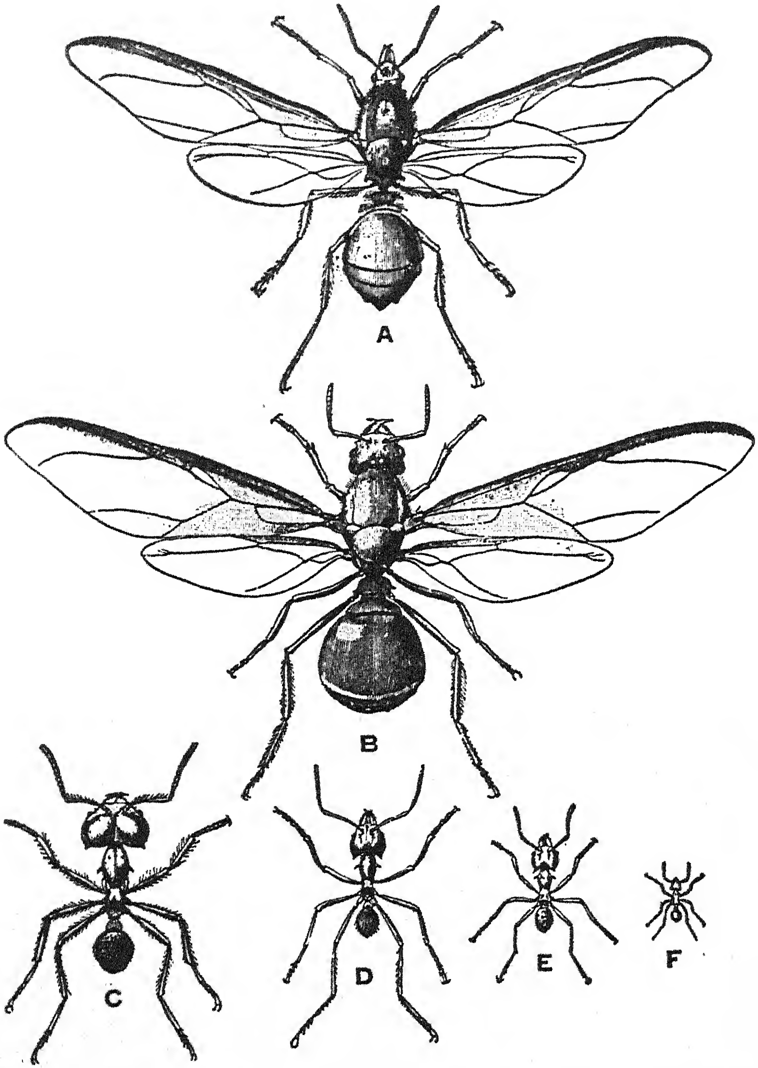


FIG. 169. Polymorphism in ants as illustrated by the adult forms of *Atta* (*Œcodoma*) *cephalotes* taken from a single nest. A, male; B, winged female; C–F, various form unwinged; C, so-called soldier; D, large worker; E, smaller worker; F, smallest nurse worker. All equally magnified one and a half times. (From the Cambridge Natural History.)

in case of some cataclysm does a colony come to an end; for when a queen dies, new queens take her place and a single dynasty may continue for centuries.

D. Commensalism

Many other animals besides ants live in ant galleries. Ants have their domesticated pets of various kinds, some of which are doubtless more of a nuisance than anything else. These ant associates are usually called MYRMECOPHILES (meaning literally "ant lovers"). They share with ants all of their advantages. Some of these act a useful rôle as scavengers, others are mere camp followers, and some are actual thieves and parasites. Interesting types of commensals not infrequently found associated with ants are mealy bugs and plant lice. Ants actually domesticate these creatures much as man has domesticated cattle, and for similar purposes. Thus the corn-root aphids feed upon the juices of tender roots and excrete as a by-product drops of sweet fluid known as honeydew. This the ants eagerly lap up. So attached to aphids are ants that they capture them aboveground and carry them to their galleries. Thus the aphids are protected from their enemies and breed prolifically within the domain of the ants, acting as "ant cows."

E. Slavery

Some species of ants, as the result of overspecialization, have come to produce only the soldier type of worker. These become wonderfully efficient as fighters and raiders, but cannot do the ordinary duties of the colony. To supply this very obvious deficiency, the soldiers raid the colonies of less specialized species of ants, capture, and carry home their pupæ. When the latter emerge as workers, they play the same rôle in their captors' home as they would in their own, not only feeding the young of the slave makers but feeding also their queen and the soldiers. When these workers diminish in numbers through natural or accidental death, a new supply is obtained by raiding another colony. The slave makers are utterly dependent upon slaves, and in a sense are parasites on the enslaved species. Certain other types of slave makers are less highly specialized in that they can carry on without slaves, but rarely do so.

F. Peculiar Feeding Habits among Ants

One of the most interesting of the feeding habits of ants is that exhibited by LEAF-CUTTING ANTS (Fig. 170, 2). These industrious denizens of tropical America cut off the leaves and flowers of succulent plants, carry them to their underground chambers, where they chew them up to furnish culture beds for certain kinds of fungi. The fungus is perpetuated by means of spores carried in a specialized head fold, or pouch, and is passed on to new colonies by queens or founders. A pure culture of edible fungus is thus kept up by a given species, while different species of leaf-cutter ants rear different species of fungi.

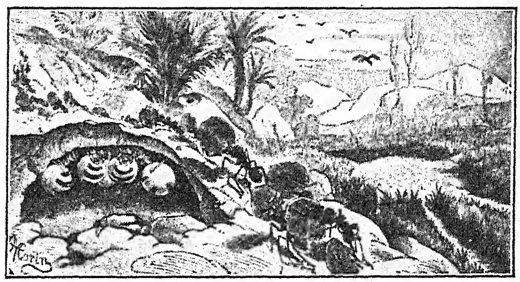

1 2

FIG. 170. Honey ants and leaf-cutting ants. (From Brehm.)

Another very odd feeding adaptation is that found among HONEY ANTS, common in Mexico and our own Southwest (Fig. 170, 1). Certain of the workers make of themselves veritable honey sacs. These specialized individuals feed gluttonously upon honey until their abdomens become swollen up into globular sacs many times as large as the rest of the body. In Mexico these honey glutted ants are prized as a confection. The value of this habit for the ants is that it enables them to store up for general colony use large amounts of a favorite food during periods when it is normally unobtainable. The honey-filled individuals remain in a state of dormancy and do nothing but act as storage vessels.

G. Ant Societies and Human Societies Compared

W. M. Wheeler, from whose classic work, *Ants: Their Structure, Development, and Behavior,* these facts are gleaned, interestingly compares ant societies with human societies. He notes that ant societies are conducted by the female sex; while the males are merely the short lived mates of the queen, live a lazy life, and have no influence in the management of the community. The guiding spirits of the whole colony are the workers—sterile females; they

constitute a society of amazons. In contrast with this situation, human society, until recently at any rate, has been conducted chiefly for and by the males. Human communities of the modern sort are artificial aggregations of unrelated individuals, each of which has a capacity for a considerable range of activities, but usually becomes specialized, either of his own accord or through economic pressure, along some one line of communal service. The fact that man's lot in life is so often artificially determined gives rise to unrest and discontent. In the case of ants, however, affairs are quite different: each individual is born with certain morphological characters and a certain instinctive equipment that settles once for all its status in life. Thus all is harmony and coöperation. A revolution in an ant community is inconceivable, for each ant is her own ruler and there are no regulations imposed from without or by a centralized authority. An ant community may be looked upon as a sort of socialistic anarchy.

SUMMARY

1. Ants belong to the Phylum Arthropoda, Class Insecta, and Order Hymenoptera, one of the most specialized of insect orders.
2. The ants exhibit complete metamorphosis, the grublike larva going into a pupal stage during which radical changes take place. From the pupa emerges the adult, or imago.
3. The ants have become perhaps the most successful of insects due to their subterranean dwellings, their polymorphism and their social organization.
4. The ant society, as was indicated in Chapter V, may be regarded as a complex life unit integrated by bonds of instinct.
5. There is a specialization of castes within the society, which involves division of labor among specialists and hence increased efficiency for the social unit.
6. Various types of commensals live in the dwellings of ants, forming a complex ecological community that may be regarded as a still more elaborate type of life unit than the society.
7. Some of the commensals are purely parasitic, others symbiotic.
8. Slavery involves another type of communal organization and gives rise to another type of complex life unit.
9. Ants exhibit many specialized modes of feeding.
10. Ant societies and human societies are compared and contrasted.

CHAPTER XXVIII

INSECTS AND DISEASE

(PHYLUM ARTHROPODA)

A. Warfare between Insects and Man

In all the world of life the insects seem to be preëminent for numbers of species, over 500,000 species having been named and probably as many more being still unidentified. It would be strange, then, were all of these favorable to human welfare. As a matter of fact, man and the insects are rivals for dominance in the modern world; they compete for the same food materials and the same "place in the sun." There is warfare between them: man battles the insects and the insects attack man, his domestic animals, and his crops. Perhaps the most serious modes of attack of the insects upon man are carried on by various types of disease carriers—mosquitoes, flies, bugs, lice, and fleas.

B. Modes of Disease Transmittal

Some insects either in the adult state or during the larval period actually invade and feed upon human tissues. Thus, certain fleas of tropical countries burrow beneath the skin and breed there, causing sores and destroying tissue. Strictly speaking, this is a case of parasitism rather than disease, though the distinction between the two is by no means clearly defined. By far the most important relation of insects to disease has to do with their rôle as carriers of pathogenic bacteria and Protozoa. The insect itself is often diseased and transmits the germs of disease by biting human beings or by contaminating their food. A few of the best known instances of the rôle of insects as disease carriers will now be discussed.

C. Mosquitoes and Malaria

One of the greatest achievements of modern medical science had to do with the discovery of the rôle played by the mosquito in the transmittal of malaria. Formerly, malaria was supposed to be the result of bad air or bad water; now, it is known to be the result

of the invasion of a minute protozoan parasite—somewhat like a small Amœba—that invades and destroys the red blood corpuscles. A single organism enters a red blood cell, feeds upon its protoplasm, and multiplies. After the whole blood cell is consumed the numerous progeny escape into the blood stream and attack other blood cells. On the rupture of the dead corpuscle metabolic by-products, toxic in character, escape into the blood and cause the symptoms of chills and fever.

If a human being infested with malarial organisms is bitten by a certain kind of mosquito belonging to the genus Anopheles (Fig. 171, **A**), the latter draws into its stomach a small amount of human blood together with its contained malarial organisms. These go on living in the mosquito, passing through certain phases of their complicated life cycle, which is described and illustrated in Figure 172. The mosquito thus becomes diseased, and when it bites another human being, it first injects a little infected saliva into the wound. This serves to prevent the coagulation of the blood and at the same time infects the blood of the new host. Malaria can be prevented by breaking the train of transmittal, and this may be accomplished by preventing the breeding of mosquitoes or by screening houses so as to exclude mosquitoes. In cases where rabbits or other mammals act as an intermediate host alternative to man, it is much more difficult to break the train of transmittal.

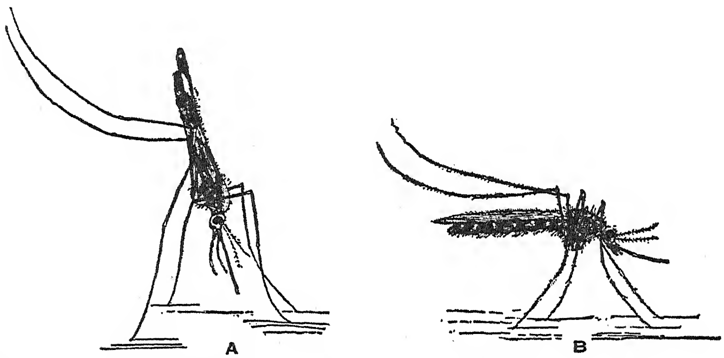


FIG. 171. **A**, position of malaria mosquito (*Anopheles*) when at rest. **B**, position of common house mosquito (*Culex*) when at rest. (After Howard.)

Quinine is a specific remedy for malaria. When taken in sufficient doses at the time when young parasites are free in the blood, these may be killed without injuring human tissues.

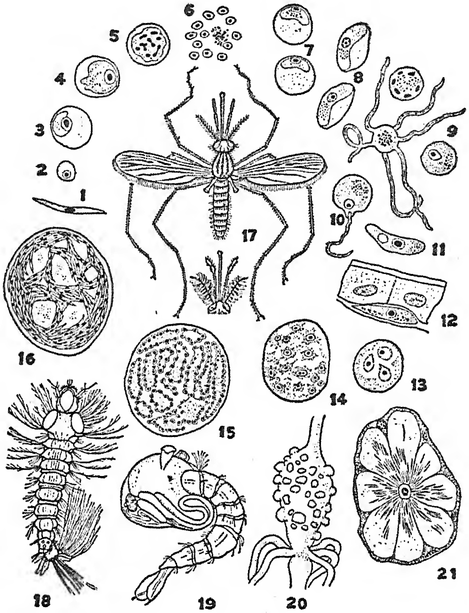


FIG. 172. *Diagram of the life history of the malarial parasite* (*Plasmodium falciparum*). The life cycle may be divided into (*a*) *schizogony*, the formation of self-infective spores in the human blood (stages **1–6**), (*b*) *sexual generation* or the formation and conjugation of the male and female gametes (stages **7–10**). During the early part of this phase of the life cycle the parasite is transferred to the mosquito, (*c*) *sporogony*, the formation of cross-infective spores in the invertebrate host, the Anopheles mosquito (stages **11–16**). **1,** sporozoite, a spore introduced into the blood stream of man by the bite of the mosquito; **2,** merozoite, spore formed in the blood of man for infecting new red blood corpuscles; **3, 4,** two amœboid stages in the growth of the parasite within red blood corpuscles; **5,** mature parasite with nucleus dividing up to form merozoites; **6,** merozoites free in the blood by breaking down of the red blood corpuscle; **7, 8, 9,** formation of male and female gametes; **10,** male gamete penetrating female gamete; **11, 12,** active zygote which bores its way through epithelial wall of stomach of mosquito, where it comes to rest and encysts; **13,** encysted zygote with three nuclei; **14,** encysted zygote with numerous sporoblasts; **15,** a cyst showing sporozoite formation during which the nucleus of each sporoblast has divided into numerous nuclei, each surrounded with a little protoplasm, thus forming a sporozoite; **16,** a cyst filled with ripe sporozoites ready for transmission to the salivary glands of the mosquito; **17,** Anopheles mosquito, female above, head of male below; **18,** larva of Anopheles mosquito; **19,** pupa of Anopheles mosquito; **20,** stomach of Anopheles mosquito showing cysts of malarial parasite on outer wall; **21,** sporozoites in the secreting cells of a lobe of the salivary glands. (Redrawn after Pfurtscheller wall chart.)

D. Mosquitoes and Yellow Fever

Much more deadly than malaria is the disease yellow fever, formerly one of the most dreaded of human plagues, now almost entirely eradicated. While the American troops were in Cuba a plague of yellow fever struck them so severely that a Yellow Fever Commission, headed by ***Dr. Walter Reed*** was appointed to investigate the situation. It was found that the fever was transmitted by one species of mosquito and in no other way; that, as in the case of malaria, the bite of the mosquito serves both to pick up the disease and to inject it into a second person. The commission then proceeded to drain marshes or to pour crude oil on stagnant ponds where mosquitoes were wont to breed. In this way yellow fever was practically eradicated. If similar precautions were to be taken in the numerous malaria infested parts of our country, this less dreaded, but none the less serious and often fatal, disease could be entirely wiped out. A few millions of dollars would be sufficient to accomplish this; and it will be done when public opinion becomes sufficiently aroused. The total eradication of malaria from the United States would be one of the greatest accomplishments the Federal Government might boast.

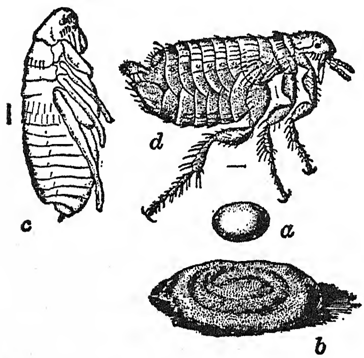


FIG. 173. Cat and dog flea, *Ctenocephalus canis.* *a,* egg; *b,* larva in cocoon; *c,* pupa; *d,* adult. (From Howard, Circ. 108, Bur. Ent., U. S. Dept. Agric.)

E. Fleas and the Plague

The history of ancient and of modern times is punctuated by the recurrence of a terrible affliction known as PLAGUE, sometimes called the "black death." One epidemic of this disease during the fourteenth century spread over nearly the whole world and caused the death of as many as 25,000,000 people—a very large percentage of the whole population. In those days nothing was known as to the cause of the disease and less about its treatment or cure. Now it is known to be due to a minute germ and to be transmitted from rats, mice, and other small rodents, through the intermediary aid of fleas (Fig. 173).

The diseased rats are bitten by fleas and the same fleas then bite human beings, injecting disease germs into their blood. Plague may be checked by destroying rats and other flea infested animals and by isolating plague stricken human beings to prevent the passage of fleas from them to other subjects.

F. Lice and Typhus

The discovery of the rôle of lice in the transmittal of typhus was made by ***Dr. Henry Taylor Ricketts,*** who died a martyr's death while engaged in studying this dread disease in Mexico. The situation is much like that in the case of plague. Trench fever—somewhat similar to typhus—is known to have a similar etiology. Mites and ticks, while not insects, are responsible for various other diseases such as itch, mange, relapsing and Rocky Mountain fever.

G. Flies and Typhoid Fever

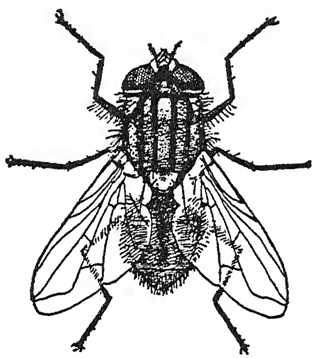


Fig. 174. House fly, *Musca domestica.* (From Howard, Circ. 71, Bur. Ent., U. S. Dept. Agric.)

The common house fly (Fig. 174) is one of the greatest nuisances with which man has to contend. This insect has very filthy habits, feeding upon and breeding in all sorts of decomposing organic matter. When they alight upon the excreta of typhoid patients, they pick up upon their padded feet countless typhoid germs, which they leave upon exposed food or cooking utensils. Thus they serve as the most effective disseminators of typhoid. The "swat the fly" campaign is therefore one of great importance. Proper sanitation, such as adequate sewage disposal, screening of houses, and covering of garbage, are known to be important prophylactic measures.

H. Flies and Sleeping Sickness

One of the most terrible of tropical diseases—the so-called sleeping sickness—is known to result from the bite of a blood-sucking insect, the tsetse fly (Fig. 175). The organism directly responsible for the disease is a flagellate protozoan—a trypanosome which lives in the blood. Horses, mules, and camels are infected

with this disease, and it is transmitted from these animals to man or from man to man through the bite of the fly. The fly lives in marshy thickets and it is possible to render any limited region

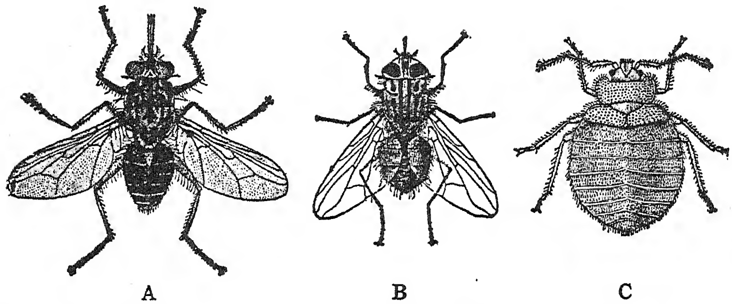


FIG. 175. Sucking insects that carry disease germs. A, tsetse fly, which carries the germs of sleeping sickness; B, stable fly; C, bedbug. (After Howard.)

comparatively safe by cutting down all neighboring thickets, especially those near the haunts of horses.

The future history of mankind will doubtless be marked by his conquest of insects and, incidentally, of the diseases that are associated with insects and allied forms. It is not too much to hope that the next hundred years will see this war carried to a successful issue.

SUMMARY

1. There is a war on between man and the insects. No one knows which has the upper hand at present.
2. One of the modes of warfare has to do with the fact that insects transmit infectious diseases to man.
3. The Anopheles mosquito is responsible for transmitting the malaria parasite from person to person. The mosquito harbors the parasite and in the tissues of the mosquito several stages of the life cycle of the parasite are passed. The life cycle is completed in the blood of man.
4. Another species of mosquito is an intermediate host for the yellow fever parasite.
5. Fleas, flies, and lice are also important as transmitters of various serious human diseases.

CHAPTER XXIX

ROUNDWORM PARASITES IN MAN

(PHYLUM NEMATHELMINTHES)

A. Parasitism in General

If one were to list all free-living animals in the world in one column and all the parasites in another, the parasite list would be much longer than that of the independents. That this is true is readily deducible from the fact that practically every organism has upon it or within it at least one, and usually several, species of parasites. Even the parasites themselves have parasites within them. Thus there is a hidden, ugly world of parasites which doubtless outnumbers that of the host species.

The usual effects of extreme parasitism upon the parasite are that those organs and systems associated with a free life and the earning of an independent living tend to degenerate or to be entirely lost, and instead, there appear various kinds of suckers, hooks, and other holdfasts by means of which the parasite clings to the host. Associated with the fact that parasites are so commonly fixed in position and cut off from association with members of their kind, they are very commonly HERMAPHRODITES (male and female in one). Again, because they very frequently occupy two or more species of hosts, the vicissitudes of life are so great that it is necessary to produce very large numbers of offspring. As a result of this the relative bulk of reproductive tissues as compared with that of the body as a whole is greatly increased.

Of all the animal phyla, three stand out preëminently as parasitic phyla: Protozoa, Nemathelminthes, Platyhelminthes. By no means all members of these phyla are parasitic, but undoubtedly over 90 per cent of all animal parasites are to be found in these three phyla. Among other phyla that exhibit parasitism should be mentioned especially Arthropoda, Mollusca, and Annelida.

Of the three phyla of animals that are outstandingly parasitic, the Nemathelminthes seem to show less difference between the

parasitic and free-living species than do the others. They show little degeneration, only occasional hermaphroditism, and but few specialized organs of attachment; yet they are blind, have no special organs of locomotion, and produce very large numbers of offspring, as many as 60,000,000 eggs having been estimated as the product of a single nematode.

The Nemathelminthes are important to man chiefly because they invade the human body and produce various morbid symptoms that are called diseases.

B. The Abundance of Roundworms

In a previous chapter, under the caption, "The Inhabitants of Two Square Feet of Soil," a paragraph (p. 130) was quoted from *N. A. Cobb,* a world's authority on nematodes. That paragraph would bear reading again in this place.

There are thousands of species of parasitic nematodes and other roundworms, and still larger numbers of free-living species. It has been estimated that there are more than 80,000 nematode species parasitic on vertebrates alone, to say nothing of those infesting other invertebrates. "Numerous as the parasitic species are," says Cobb, "it is certain the number of species of nematodes living free in soil and in water far outnumber them. . . . There must be hundreds of thousands of species." A group so widespread and numerous deserves attention even in a general course.

C. Characteristics of the Phylum Nemathelminthes

As the name indicates, these are long, slender worms with the body cylindrical instead of being flattened as it is in the flatworms. They differ from the flatworms also in the following ways: The intestinal tract has two openings, mouth and anus, at opposite ends of the body; there is a dorsal as well as a ventral nerve cord, the two cords being united by several commissures; they are nearly all diœcious (have separate male and female individuals); there is a total absence of cilia. They resemble the flatworms in having no specialized circulatory or respiratory systems.

The roundworms differ from the annelids in the following respects: They are unsegmented; they have no true cœlom, but merely a space between the mesoderm cells of the body wall and the endoderm cells of the intestine; they have no special organs of

circulation and respiration; they have a dorsal as well as a ventral nerve cord; and they have no locomotor appendages.

The method of cleavage in most of the roundworms is decidedly determinate, which makes them in that respect more like the annelid-arthropod group; the mesoderm is set apart as early as the eight-cell stage, a fact that further seems to link the Nemathelminthes with the annelid-arthropod series. These two characteristics, together with the lack of any true cœlom, seem to prohibit the alignment of this phylum with either main series. We obtain, however, a suggestion from a group of primitive wormlike forms known as Chætognatha (the arrow worms), which resembles the Nemathelminthes more closely than any other group. These forms give rise to the cœlom in a fashion characteristic of the echinoderm-chordate series, i.e., by cutting off pouches from the archenteron. It seems probable therefore that the cœlomless Nemathelminthes of today may have originally had an enterocœlic cœlom, but have lost it through degeneration.

Out of the many thousands of species of roundworms we shall choose, for reasons that will be obvious, two of the best known species: *Ascaris lumbricoides* and *Trichinella spiralis*.

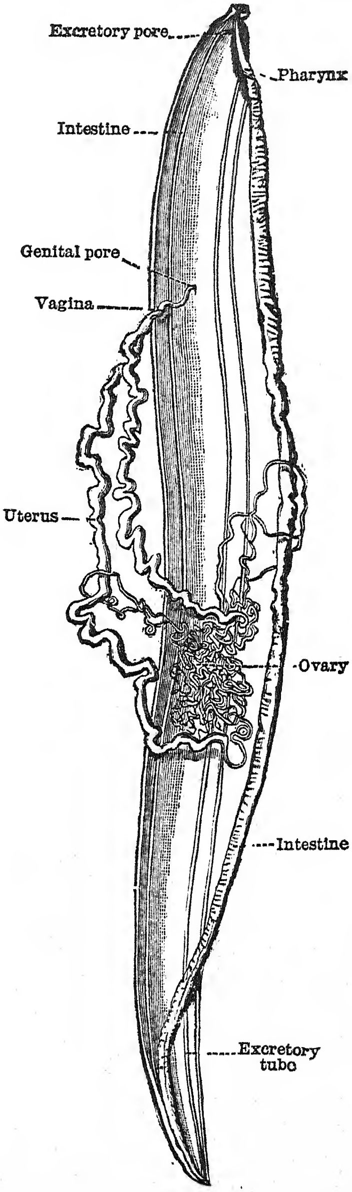


FIG. 176. A female *Ascaris lumbricoides* cut open and internal organs spread out to view. (From Shipley and MacBride.)

1. *Ascaris lumbricoides*

Various species of the genus Ascaris are parasites in the intestines of mammals. *A. megalocephala* infests the horse, *A. suiela* occurs in the pig, while *A. lumbricoides* lives in the intestines of man. Because of the bearing of the last species upon the practice of medicine we shall confine our account to it alone.

Ascaris lumbricoides (Fig. 176) is a slender worm, the females of which are about 8 to 16 inches long and about one-fourth inch

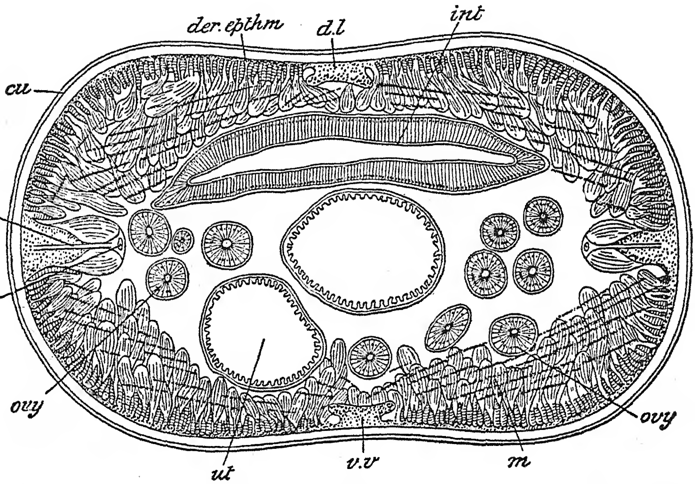


FIG. 177. Transverse section of *Ascaris lumbricoides*. *cu*, cuticle; *der. epthm*, dermal epithelium; *d.l*, dorsal line; *ex.v*, excretory tube; *int*, intestine; *lat.l*, lateral line; *m*, muscular layer; *ovy*, ovary; *ut*, uterus; *v.v*, ventral line. (From Parker and Haswell.)

in diameter. The male is much smaller. The mouth is at the anterior end and has three liplike lobes, one median-dorsal and two ventrolateral (Fig. 178, *b* and *c*). The anus is at the posterior end and opens by a transverse slit bounded by lips. This opening is also the opening for the reproductive ducts.

The body wall (Fig. 177) consists of a delicate, transparent cuticle (*cu*), a protoplasmic layer (*der. epthm*) containing scattered nuclei and fibers imbedded in a continuous substratum. This is, of course, a SYNCYTIAL ECTODERM. The next layer is a single layer of very peculiar muscle cells, or fibers. The contractile part of each cell is spindle-shaped, but from the side of each fiber comes off a sort of bladderlike enlargement with a nucleus extending

into the false cœlom. The muscle layer is divided into four separate ribbons by means of four thickenings of the ectoderm known as DORSAL, VENTRAL, and LATERAL LINES.

a. **The Digestive Organs.**—These consist of the MOUTH, PHARYNX (or STOMODÆUM), the INTESTINE, the short RECTUM, and the ANUS. The food consists of the partially digested semifluid contents of the intestine of the human host, which is sucked up by the muscular movements of the pharynx.

There is a very distinct space, the FALSE CŒLOM, between the body wall and the intestine. The viscera lie very loosely in this, not slung by mesenteries or supported by septa.

b. **Excretory System.**—Two longitudinal canals comprise this system. They are separate posteriorly but unite anteriorly into

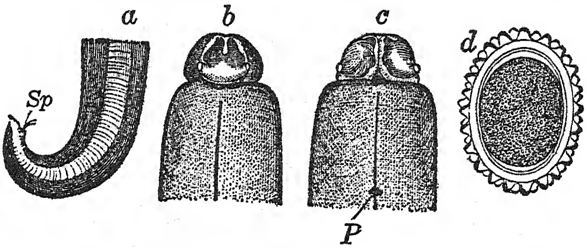


FIG. 178. Parts of *Ascaris lumbricoides*. ***a,*** hind part of male with two penial setæ (*Sp*); ***b,*** anterior end from dorsal side showing dorsal lip and two papillæ; ***c,*** same from ventral side showing two lateral ventral lips; ***d,*** egg with external membrane; ***P,*** excretory pore. (From Sedgwick.)

a single short canal that opens on the ventral side near the mouth by a single opening (EXCRETORY PORE). This system differs from that of the flatworms in having no cilia or flame cells.

c. **Nervous System.**—The nervous system consists of a flat nervous ring about the pharynx from which there are six branches forward and six branches backward. Two backward branches, one dorsal and one ventral, are larger than the others and run from end to end of the worm, being connected at intervals by transverse commissures.

d. **The Reproductive Organs.**—In the males, the TESTIS is a long, coiled tube, about the diameter of fine sewing thread. This passes into the VAS DEFERENS which in turn enlarges into a distended SEMINAL VESICLE. This opens into the rectum near the anus. Near this opening are paired muscular sacs, containing PENIAL SETÆ (Fig. 178), organs of copulation. In the females

(Fig. 176), the OVARIES are paired, each ovary being long and coiled and passing into a long enlarged duct, the UTERUS. The two uteri unite into a short muscular VAGINA, that opens on the ventral side about one-third way back from the head.

The eggs are fertilized in the uterus of the worm in enormous numbers. Each egg becomes coated with a layer of chitin (Fig. 178, *d*), which prevents it from being injured by the digestive fluids of the host and allows it to pass unharmed out of the body with the fæces. It is transmitted directly to other hosts by means of contaminated drinking water or through soil adhering to food. The eggs hatch in the intestine of the new host, and there the worms grow to a large size at the expense of the host. A person infested with a considerable number of Ascaris is likely to exhibit extreme emaciation, which may end in death.

2. *Trichinella spiralis*

Trichinella is one of the most dreaded of human parasites. It is responsible for the terrible disease, TRICHINOSIS, which is so often

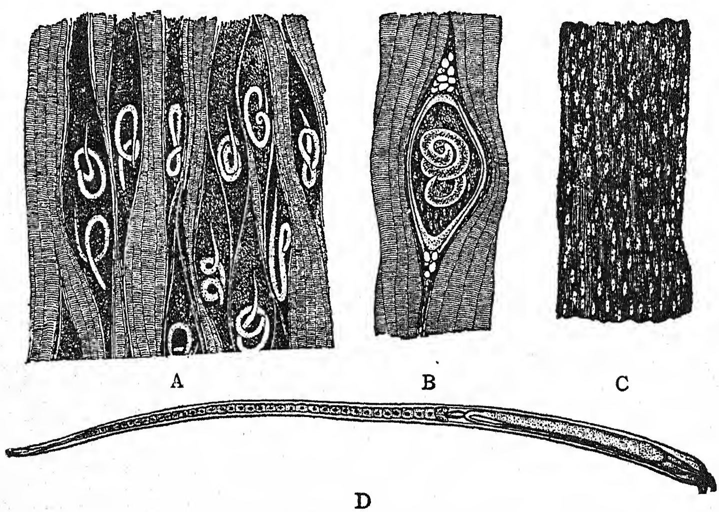


FIG. 179. *Trichinella.* A, larvæ among muscle fibers, not yet encysted; B, a single larva encysted; C, piece of pork natural size containing many encysted worms; D, adult, much enlarged. (After Leuckart.)

fatal. The worms are very tiny, the females (Fig. 179, B) hardly more than an inch in length and the males much smaller (Fig.

179, D). In the adult condition this worm lives in the intestinal canal of man, the pig, and other mammals. The adult females, which give birth to living young, burrow out through the wall of the intestine and enter various lymphatic vessels, where they release their broods of young. Thousands of these become distributed passively about the body in lymph and blood. When they reach their favorite region, the voluntary muscles, they burrow in, each minute worm penetrating a single muscle fiber, where it coils up (Fig. 179, A). The irritation causes the muscle fiber to degenerate and form a cyst about the coiled up worm larva. The host then shows various severe morbid symptoms upon which we need not dwell. In severe cases there may be as many as 100,000,000 encysted worms in a single subject. Trichinosis in man is usually the result of eating infected (measly) pork, which has not been cooked sufficiently to kill the parasites.

D. Other Roundworm Parasites in Man

Among many other roundworms that are of economic importance because they are the cause of human disease and suffering, are *Filaria bancrofti*, which produces the disease ELEPHANTIASIS, and *Necator americanus*, the cause of the disease called HOOKWORM, that has affected millions of human beings and has caused the death of many and a markedly lowered efficiency in all who are afflicted with it.

Research in connection with various educational institutions and medical organizations has served to reveal the life histories of these pests and has shown us how the diseases may be wiped out. Much good has been done already and we have every reason to hope that at no very distant time man will free himself from these enemies within his body.

SUMMARY

1. There are probably more parasites among animals than independent organisms, for every independent type has its parasites.
2. Parasitism is usually associated with degeneration of those organs adapted for independent living and the specialization of organs for holding fast to the host and feeding upon its tissues. Because of their fixed positions most parasites are hermaphroditic.
3. Roundworms belong to the Phylum Nemathelminthes. They are exceedingly numerous. Some are free livers, others parasitic.
4. Roundworms differ from flatworms in having both mouth and anus,

both dorsal and ventral nerve cord, no cilia, separate sexes (diœcious), etc.

5. Roundworms differ from annelids in having no true cœlom, no definite circulatory system, no appendages, no segmental organization, a dorsal as well as a ventral nerve cord, etc.

6. Two types of parasitic roundworms, Ascaris and Trichinella, are described in some detail.

CHAPTER XXX

THE STARFISH

(PHYLUM ECHINODERMATA)

A. Status of the Phylum Echinodermata

This phylum is at present, and has been since early Palæozoic times, a successful group. There exists a high degree of diversity of form, habit, and habitat among the echinoderms, and they are very abundant and widespread. From the first they have been exclusively marine forms of moderate size. They are most strikingly distinguished from most other groups of animals by their star-shaped, or radiate, body form, a condition especially plainly seen in the starfishes, brittle stars, and crinoids, but less obvious in the sea urchins and sea cucumbers.

The radial symmetry of the starfish and its relatives is not in any true sense equivalent to the radial symmetry of the Cœlenterates, but is merely a secondary distortion of bilateral symmetry, as is shown in a subsequent section of the present chapter.

The adults, largely on account of their secondarily developed radial form, bear scarcely any resemblance to any other animals. Hence the group seems to stand apart as though unrelated to any other phylum. Their embryonic and larval history, however, bears many fundamental resemblances to that of some of the lower members of the Phylum Chordata, notably Balanoglossus and its relatives.

The echinoderms and the lower chordates are similar in the following respects:—They are characteristically indeterminate in cleavage; the mesoderm is derived from a proliferation of cells around the lip of the blastopore; the cœlomic cavities are derived from paired out-pouchings of the archenteron; the blastopore remains the functional anus and a new mouth is established secondarily near the anterior end of the archenteron; and the larvæ of some of the echinoderms and those of some of the chordates are extremely similar.

It is because of these fundamental homologies that some leading

zoölogists feel justified in placing the echinoderms and the chordates together in the same main branch of the diphyletic tree. This is also why in this book the echinoderms are placed next to the chordates.

B. General Morphology of the Starfish

1. *External Characters*

The visitor to the seashore finds the starfishes among the most interesting of the novelties encountered. They are found in considerable numbers along nearly all of the world's seacoasts, being especially abundant wherever the coast is rocky; for starfishes are fond of rocky bottoms.

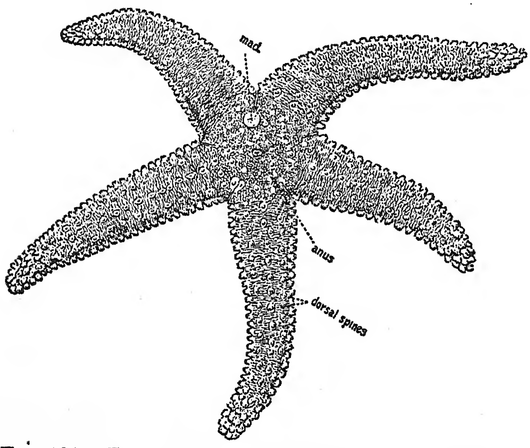


Fig. 180. The starfish, *Asterias rubens*, seen from the aboral surface. *mad*, madreporite. (From the Cambridge Natural History.)

Two main divisions of the body are to be distinguished, the CENTRAL DISK and the ARMS, or RAYS, which are usually five in number (species with six, seven, or even twenty or more rays are known). Starfishes are usually seen with the mouth side (ORAL, or ACTINAL SURFACE) in contact with the substratum, and the anal side (ABORAL, or ABACTINAL SURFACE) chiefly in view.

The ABORAL SURFACE (Fig. 180) has a spiny or rugose appearance, owing to the presence of numerous SPINES, BRANCHIAL PAPILLÆ, and PEDICELLARIÆ. On the central disk and situated near the angle made by two of the rays is a porous plate, the MADREPORIC PLATE, which acts as a filter for the water-vascular system.

The ORAL SURFACE (Fig. 181) is quite different in appearance. The mouth is situated at its center and is surrounded by a soft membrane, the PERISTOME. Running from the mouth out to the ends of the five arms are the AMBULACRAL GROOVES, so called be-

cause they are largely filled with tube feet, the chief locomotor organs of the group.

2. *The Skeleton*

The skeleton of the starfish, unlike that of most animals with an external armor, is developed in the DERMIS, or deeper skin, and

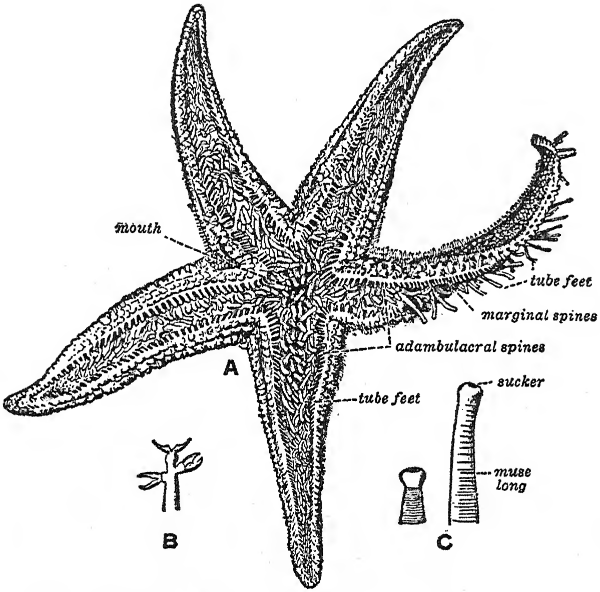


FIG. 181. A, the starfish, *Asterias rubens*, seen from the oral surface; B, an adambulacral spine, showing three straight pedicellariæ; C, a tube foot expanded and contracted. (From the Cambridge Natural History.)

is covered over by a thin EPIDERMIS, or outer skin. It is composed of numerous small calcareous plates bound together by means of connective tissue so as to form an intricate basketwork. The spines are quite short as compared with those of the sea urchins (distant cousins of the starfishes); and often they have rounded or knobbed ends.

Around the bases of the spines there are numerous tiny modified spines, called PEDICELLARIÆ, that have a structure and mechanical operation like pliers or pinchers (Fig. 181, B). These little organs function in a variety of ways, their chief duties being to protect the delicate branchial papillæ from being browsed upon

by small carnivorous crustaceans and the like, to aid in the capture of food, and to keep the delicate skin free from dirt and débris. Each pedicellaria is an automatic weapon of offense or defense and is set into action by definite stimuli. When, for example, a small crustacean walks over the surface of the starfish, its legs come in contact with several groups of pedicellariæ. These reach forth their snapping pinchers and many of them succeed in grasping hairs on the invader's appendages. If a struggle ensues, many more pedicellariæ come to the rescue until the struggle ceases because the captive is held rigid by myriads of tiny clamps, for once they have closed upon their prey they are like bulldogs for tenacity. When all struggle ceases, the pedicellariæ release their holds and the tubefeet take over the duty of seizing and passing the prospective luncheon from hand to hand, or rather from foot to foot, over the edge, and down to the mouth.

While the skeleton renders the starfish rather stiff and unyielding to the touch, it is not entirely rigid. In fact, numerous muscles which are attached to the inner surfaces of the plates are capable of moving the whole body, or any part of it, slowly and deliberately into any position demanded by the exigencies of life.

3. *Internal Organization*

a. The Cœlom.—If one cuts through the skeleton, he will note that the internal organs (viscera) lie rather loosely in a capacious body cavity, the cœlom. This large cavity is lined with a smooth PERITONEAL MEMBRANE and is filled with CŒLOMIC FLUID, which, except for a small quantity of suspended albuminous matter, has about the consistency and chemical content of sea water. The cœlomic fluid plays the rôle of blood, for there is no true system of blood vessels. Oxygen is taken into the blood and carbon dioxide eliminated into the sea water through the thin walls of the BRANCHIAL PAPILLÆ, which consist of fine processes of the cœlom thrust through the interstices of the skeleton and protruding on the outside. Certain AMŒBOID CELLS, which appear to function quite like the leucocytes, or white blood cells of our own blood, are rather abundant in the cœlomic fluid. Their duty seems to be that of ingesting and digesting waste matters that cannot be eliminated in liquid form. When old or exhausted, these cœlomic corpuscles work their way through the thin walls of the branchial papillæ and undergo dissolution in the sea water.

b. Water-vascular System.—This important and unique system (Fig. 182) takes its origin from one of the larval cœlomic cavities known as the HYDROCŒLE, and differentiates into an extremely intricate system of water tubes and sacs, the like of which is not found anywhere else in the animal kingdom. Water from the sea enters this system through a stony sieve, the MADREPORIC PLATE; it passes through a pressure tube with stone lined walls (the STONE CANAL) to a ringlike tube around the mouth (the CIRCUMORAL CANAL), which in turn gives off the five RADIAL CANALS, one to each arm, and is provided with bulbs (POLIAN VESICLES) which lie between the radial canals and doubtless act as pumps to force the water out into the canals. Each radial canal is provided with numerous short, lateral branches that occur in pairs and terminate each in a TUBE FOOT with its AMPULLA, a sort of syringelike bulb. Sea water is taken into the water-vascular system by means of pressure created by the inward beat of the cilia lining the water canals.

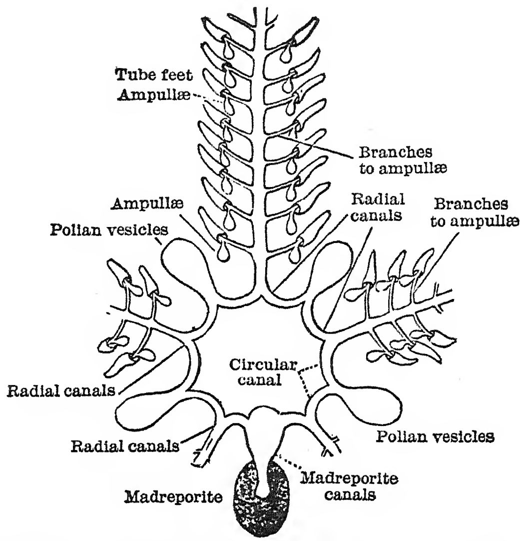


FIG. 182. Water-vascular system of a starfish. (From Parker and Haswell, after Gegenbaur.)

A large part of the cœlom is filled with the much folded STOMACH and the large HEPATIC CÆCA, or liver glands. Also, during the breeding season the gonads (OVARIES and TESTES) become voluminous and occupy most of the otherwise open space of the cavity.

C. Activities of the Starfish

Locomotion.—The main efforts of the starfish, like those of so many other animals, are concerned with the search for and the capture of food. In moving about, the tube feet (Fig. 181, **C**) and

the arm musculature together constitute the locomotor mechanism. The operation of the tube foot is simple: it is extended partly by contraction of its circular muscles and partly by the pressure exerted by the contracting muscular bulb, the ampulla. The flat end of the tube foot is pressed so firmly against some smooth surface that it acts like a vacuum cup and adheres tenaciously. Then, through the contraction of the longitudinal muscles, the tube foot shortens and in doing so exerts a pull. The combined pull of many coördinated tube feet serves to drag the body of the animal in whatever direction the tube feet may determine. Thus the feet operate the animal, not the animal the feet.

Food and Feeding Habits.—The food of the starfish consists mainly of oysters, clams, mussels, fish, crabs, and barnacles. When a starfish finds a suitable mussel, it proceeds, according to ***MacBride,*** in the following way:—

"Their mode of seizing their prey is very curious. If they are attacking a bivalve, they bend all their arms down around it, thus arching up the central portion of the body (Fig. 183). The stomach is pushed out—this being rendered possible by the turning inside out of its edges, which are loose and baggy—and wrapped round the fated mollusk. The pushing out is effected by the contraction of some muscle fibers in the body wall: these tend to diminish the space which the cœlom occupies, and as this is filled with incompressible fluid, the stomach must be pressed out. After some time has elapsed the starfish relaxes its hold and it is then seen that the shell of the mollusk is completely empty and as clean as if it had been scraped with a knife. It was long a puzzle how the starfish succeeded in forcing its victim to relax its muscles and allow its valves to open. It was supposed that the stomach secreted a paralyzing poison, but it has been conclusively proved that this is not the case, but that the starfish drags the valves of its victim apart by main force, often actually breaking the adductor muscles.

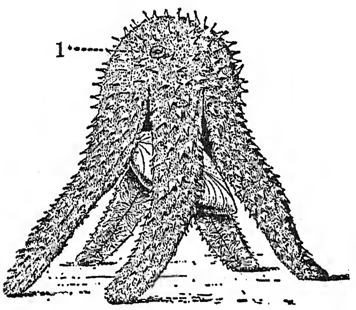


FIG. 183. View of starfish (*Echinaster*) devouring a mussel. 1, madreporite. (From the Cambridge Natural History.)

The pull exercised by the suckers is not nearly strong enough to open the valves at once, but the starfish has staying power and eventually the mussel is slowly forced open." The secret of the unusual endurance of the starfish is that its tube feet work in relays, some resting while the others work. This the mussel cannot do, for it has only one set of adductor muscles and these in the course of time become fatigued and relax. The shell once open, the abundant digestive juices of the hepatic cæca pour out upon the soft flesh of the clam and complete digestion takes place.

The Starfish a Brainless Automaton.—It may seem strange to speak of any animal so highly organized as a starfish as brainless, but the statement is literally true. The starfish, in fact, has no head, for the true head—the preoral lobe of the larva—is entirely lost in the process of metamorphosis and a new mouth breaks through into the side of the stomach. Morphologically, then, the starfish is a creature consisting of the posterior end of an organism. One would not expect much of a brain in an animal so constituted. The nearest approach to a central nervous system consists of a slender NERVE RING around the mouth. This ring gives off five RADIAL NERVE CORDS, one above each ambulacral groove. There is nothing equivalent to a central ganglionic mass, but many small ganglia are present, especially throughout the skin, and are associated with the activities of tube feet, pedicellariæ, branchiæ, and body muscles. Each of these organs is at least semiautomatic, each being provided with its own nerve cell or ganglion. The chief sense organs are the pads of the tube feet, the delicate branchiæ, and the five EYE-SPOTS, one at the tip of each arm. At best, the nerve ring and the five radial nerve bands act as coördinating organs, bringing some harmony of action out of a multiplicity of minor activities. In last analysis, however, it appears that the starfish is managed by its numerous movable parts. Speaking of the sea urchin, whose mental status is equivalent to that of the starfish, ***Von Uexkull*** explains in picturesque fashion the difference between the activities of an animal with a brain and one without: "In a dog," he says, "the animal moves the legs: in a sea-urchin the legs move the animal."

The Question of Intelligence.—After accusing the starfish of being a brainless automaton, the question naturally arises as to whether or not the animal shows any symptoms of having intelligence. Several investigators have interested themselves in this problem. ***Professor Jennings,*** for example, endeavored to teach

the California starfish some new tricks, with what success we shall presently relate. Each starfish has its own individuality, for no two of them behave just alike when they are turned upside down and have to right themselves. One uses a given pair of arms to roll over upon; another uses quite a different combination. A chosen individual is first allowed a number of trials in order that it may demonstrate its peculiar habitual method of righting himself. Then the experiment begins. The animal is turned over, and when it attempts to right itself in the preferred way, it is prevented from so doing by detaching the tube feet as fast as they reach out to gain a foothold. Only when it resorts to the use of an unfamiliar method is it allowed to proceed. After a considerable number of trials, it is then allowed to right itself several times without interference. According to Jennings, the animal has learned its lesson, for it now uses the new method in preference to the old for a number of trials, although in a few days it goes back to its original preference. The experiment seems to show that the animal has the elements of memory and a slight degree of ability to learn or to profit by experience; but various critics point out that the experiment is far from conclusive, for the constant loosening of the feet by means of a glass rod merely injures these organs for a short time so that they are not so strong or so active as the tube feet of other arms. The question of the intelligence of the starfish and its kin is still unsettled and probably will remain so until the experts can agree upon a definition of what constitutes intelligence.

D. The Development and Metamorphosis of the Starfish

The early development is quite like that of several other groups of invertebrates. Cleavage ends in the production of a typical hollow BLASTULA (Fig. 184, **1**) which is capable of swimming about by means of its cilia. This blastula is a larva, for it is capable of leading an independent life, though as yet it has no mouth and therefore cannot feed. The gastrula stage is attained by means of an inturning or invagination of the cells at the lower or vegetal pole of the blastula (Fig. 184, **2**). These cells extend up into the BLASTOCŒLE, or hollow of the blastula, as a cylindrical tube with an opening to the outside (the BLASTOPORE) and a blind end directed toward the apical end of the larva. This inner layer of cells is known as the ARCHENTERON, or primitive intestine. The GASTRULA larva (Fig. 184, **3**) now elongates; the blind end of the

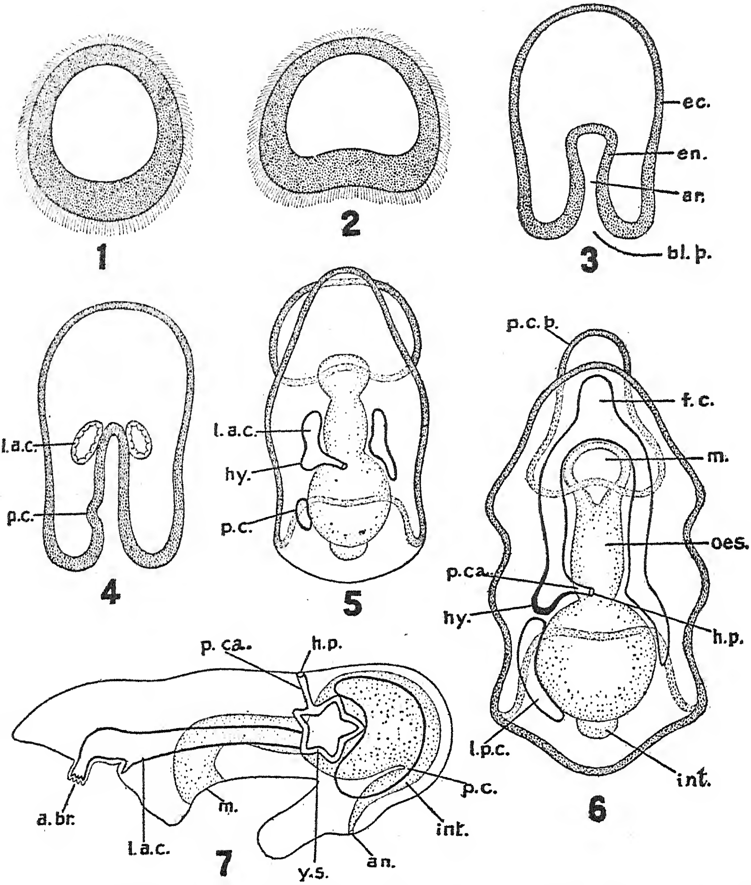


FIG. 184. Stages in the development of the starfish, *Patiria miniata* showing especially the changes from the bilaterally symmetrical larva to the radially symmetrical adult. **1**, blastula; **2**, early gastrula; **3**, late gastrula; **4**, early bilaterally symmetrical Bipennaria larva; **5**, first appearance of asymmetry, hydropore and water pore appearing on the left side; **6**, late Bipennaria larva; **7**, Brachiolaria larva showing radial symmetry established by the fanning out into radial order of the radial branches of the hydrocœle. **a.br.**, anterior brachium or sucker; **an.**, anus; **ar.**, archenteron; **bl.p.**, blastopore; **ec.**, ectoderm; **en.**, endoderm; **f.c.**, fused anterior cœlom; **h.p.**, hydropore; **hy.**, hydrocœle; **int.**, intestine; **l.a.c.**, left anterior cœlom; **l.p.c.**, left posterior cœlom; **m.**, mouth; **oes.**, oesophagus; **p.c.**, posterior cœlom; **p.ca.**, pore canal; **p.c.b.**, preoral ciliary band; **y.s.**, young starfish. (Original.)

archenteron sends out a ventral process, which meets an invagination of the ventral ectoderm (STOMODÆUM), and these two blind sacs fuse to form a new mouth for the larva, the blastopore becoming the anus. Prior to this the anterior end of the archenteron balloons out to right and left to form the first pair of CŒLOMIC POUCHES. Up to this stage the larva (Fig. 184, **4**) is strictly bilaterally symmetrical, but soon there appear signs of asymmetry, or inequality be-

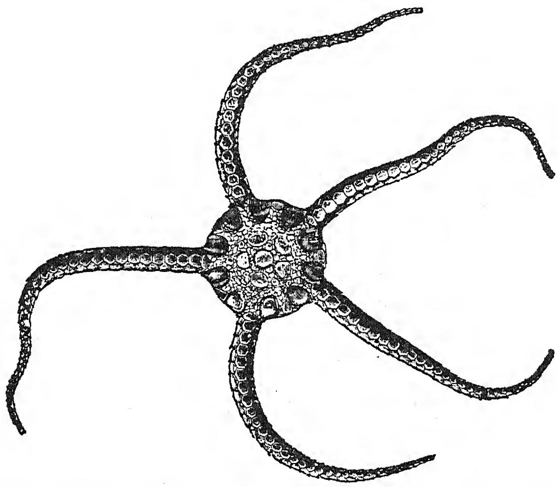


FIG. 185. Aboral view of *Ophioglypha bullata*, a brittle star. (From Shipley and MacBride, after Thompson.)

tween the two sides. The left cœlom grows much more rapidly than the right and sends to the surface a tube, called the PORE CANAL, destined to become the stone canal of the adult. Subsequently this left cœlom gives off a lateral pouch, known as the HYDROCŒLE (Fig. 184, **5** and **6**). This body lies on the left side of the larval stomach and has typically no counterpart on the right side. From the hydrocœle there are given off the five radial canals, which are at first serially arranged but soon undergo a twisting that results in the formation of the water ring and the radiating arrangement of the water-vascular system (Fig. 184, **7**). It is this series of changes that determines the adult symmetry of the starfish, for all the other organs come to group themselves about the hydrocœle and the radial canals. A new mouth forms on the side of the stomach in the middle of the water ring; a new anus forms on the

opposite side; and an entirely new axis and a new symmetry are thus attained, which have no counterpart in the Animal Kingdom.

E. Relatives of the Starfish

The Phylum Echinodermata is made up of five living and several extinct classes. The living classes are:—

Class I. Asteroidea—the starfishes, of which there is a great variety.

Class II. Ophiuroidea—the brittle stars (Fig. 185), basket stars, serpent stars. These are characterized by having a set of

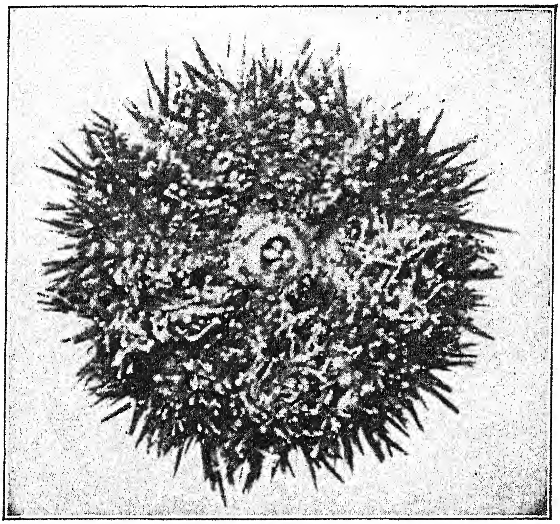


Fig. 186. A sea urchin, seen from the oral side, showing mouth and teeth of the Aristotle's lantern projecting from it. (From Clark.)

five simple or branched arms that are well supplied with muscles and are used for locomotor purposes much after the fashion of oars. These arms are sharply separated from the central disk and contain no portions of the cœlom except the radial water canals. In contrast with the Echinoidea, the aboral surface is much more highly developed than the oral, so that the true oral surface of the central disk is practically wanting. The animals are chiefly mud feeders.

Class III. Echinoidea—the sea urchins (Fig. 186), heart urchins, and sand dollars. These echinoderms differ from the two

previous classes in having the aboral surface reduced to a mere vestige, so that the ambulacral rays run nearly all the way from the mouth to the anus like meridians around a globe. Hence the tube feet are present on both lower and upper surfaces. All of the structures typical of the aboral surface are aggregated in a small area around the anus. There we find the madreporic plate, the genital openings, and the optic plates, the homologues of which are found in the starfish at the tips of the arms. The skeleton is a closely knit system of tilelike plates perforated by numerous

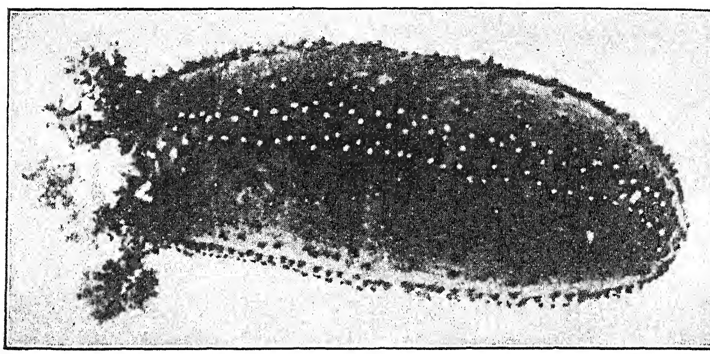


Fig. 187. A sea cucumber, seen from the side showing the specialized tube feet used as tentacles. (From Clark.)

holes for the tube feet. There is a highly specialized masticatory apparatus, the Aristotle's lantern, named after its first describer. The whole body surface, with the exception of the soft peristome around the mouth, is covered with spines, usually long and hollow, with ball-and-socket joints, and provided with muscles by means of which they may be moved about. These spines, in many species, are the chief organs of locomotion, and are used after the manner of stilts. The food of the sea urchins is chiefly seaweed, which they grind up in their food mills. There are many varieties of pedicellariæ, which are used for various purposes, some of them being provided with poison fangs.

Class IV. Holothuroidea—sea cucumbers (Fig. 187). These are like the Echinoidea in having the aboral surface reduced to a rudiment or entirely lacking, but unlike them in that they have merest vestiges of a skeleton composed of microscopic plates embedded in the skin. As a rule, they live in the mud and move

about in wormlike fashion by means of the highly developed muscular equipment of the body wall. Primarily, they are mud feeders, but, incidentally, they pick up a good many small mud-dwelling organisms. When strongly irritated, they have the habit of eviscerating themselves, shooting out their internal organs through rupture of the body wall. This is not so serious a measure

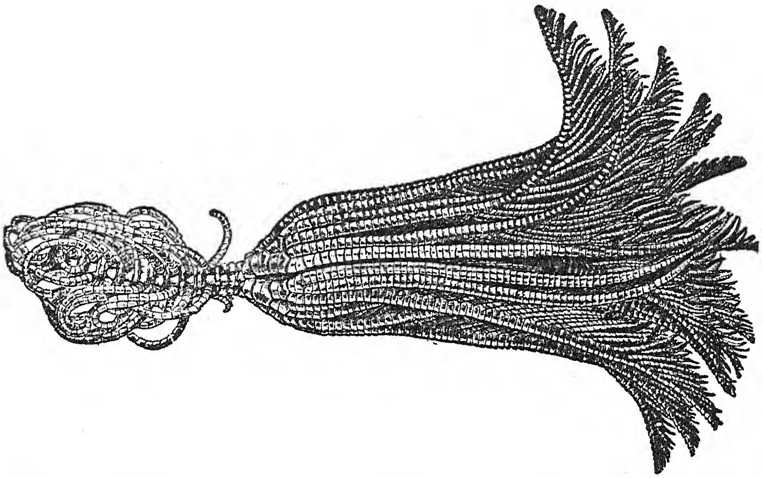


FIG. 188. A crinoid, *Pentacrinus maclearanus*, seen from the side. The arms are to the right and the stem and holdfasts to the left. (From the Cambridge Natural History.)

as it might seem, for they have the power of regenerating all lost parts quite readily.

Class V. Crinoidea—sea lilies, stone lilies (Fig. 188). In contrast with all other present-day echinoderms, these flower-like forms are typically sessile, being fastened to the bottom by means of a jointed stony stalk attached to the aboral surface. Thus the oral surface is turned upward. A few species of modern crinoids break free from the stalk, after passing a sessile larval period, and lead a free-swimming adult life. The skeleton is exceptionally heavy and massive, giving the impression of being carved out of stone. Crinoids feed by catching minute organisms in their ciliated ambulacral grooves and passing them down to the mouth. The group is an extremely ancient one, and their fossil remains constitute one of the commonest types found in the oldest fossil-bearing strata.

SUMMARY

1. The starfish belongs to the Phylum Echinodermata, Subphylum Eleutherozoa, and the Class Asteroidea, characterized by having, typically, five arms, which are not sharply marked off from the central disk and are provided with well-defined ambulacral grooves.

2. The radially symmetrical arrangement of arms and of internal organs is only secondary, not primary as in Cœlenterata. The larvæ are bilaterally symmetrical and the radial arrangement is the result of unequal growth of structures on one body half, those of the left side overgrowing the right.

3. The echinoderms are in their fundamental characters more like the chordates than any other phylum. They resemble chordates in that the cœloms are derived from paired outpouchings of the archenteron; the blastopore remains the functional anus, while a mouth breaks through near the anterior end of the archentera; cleavage is relatively indeterminate; the larvæ resemble the Tornaria larvæ of Balanoglossus, regarded by some biologists as a primitive chordate.

4. In the starfish, oral and aboral surfaces are distinguished; the mouth, ambulacral grooves, radial water canals, and tube feet being on the oral side; spines, branchial papillæ and pedicellariæ, madreporic plate, and anus, on the aboral side.

5. Of the three pairs of cœlomic cavities of the larva, the anterior pair become vestigial, the left posterior one becomes the general body cavity, the left middle one becomes the water-vascular system, and the right middle and right posterior ones become vestigial.

6. Locomotion is accomplished by concerted action of the tube feet.

7. The method of feeding involves extrusion of the stomach.

8. The starfish has no true head and no definite brain, but instead, only a nerve ring around the mouth, which serves to coördinate the activities of the five arms. Such an animal has been described as a brainless automaton.

9. The development of the starfish involves typical cleavage stages, a hollow blastula, typical embolic gastrulation, the formation of a bilaterally symmetrical larva, which metamorphoses to form a radially arranged adult. The chief agent in transforming the organization is the hydrocœle, or middle left cœlomic cavity.

PART IV

THE PHYLUM CHORDATA

CHAPTER XXXI

THE PHYLUM CHORDATA

A. General Statement

The Phylum Chordata is perhaps the most heterogeneous and diversified among animal phyla. It comprises minute sessile, colonial forms scarcely visible to the naked eye (Cephalodiscus, etc.); mud-burrowing, wormlike creatures such as the acorn worms (Balanoglossus, etc.); the degenerate sessile tunicates; Amphioxus; and a long series of true vertebrates ranging from lampreys to man.

We have a right to question the validity of throwing together such a miscellaneous assortment of creatures into one phylum. On what grounds have biologists based such a procedure?

It is claimed that all these animals possess in common three fundamental characteristics not possessed by any other animals, and that they are constructed on the same general body plan. The three distinctive characters of the chordates are NOTOCHORD, PHARYNGEAL CLEFTS (GILL SLITS) and DORSAL, TUBULAR CENTRAL NERVOUS SYSTEM. Each of these characters needs to be carefully explained:

a. The Notochord.—Typically an elastic rod, the notochord runs from the base of the brain to the end of the tail, lying dorsal to the alimentary tract and ventral to the nerve cord. Typically also, it arises from a strip of tissue originally belonging to the dorsal part of the ARCHENTERON (primitive gut). In the majority of vertebrates the notochord is present only during embryonic and larval stages and is subsequently replaced by the VERTEBRAL COLUMN that largely displaces it.

b. Pharyngeal Clefts.—These consist of a series of metameric perforations of the body wall and of the pharynx, forming passages from the latter to the exterior. Typically, the pharyngeal clefts are gill slits or branchial clefts in which lie gills, or BRANCHIÆ. The outside part of the branchial cleft is lined with ectoderm and may be provided with EXTERNAL GILLS; the inside part is lined with endoderm and may be provided with INTERNAL GILLS.

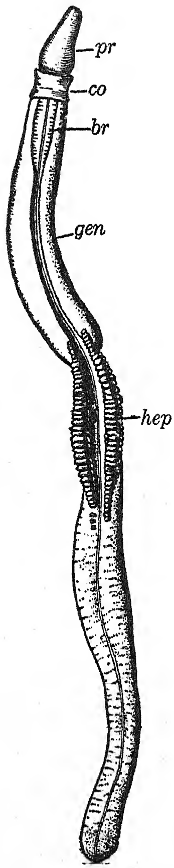


FIG. 189. *Balanoglossus.* *br*, branchial region; *co*, collar; *gen*, genital ridges; *hep*, hepatic prominences formed by hepatic (liver) cæca; *pr*, proboscis. (From Lull, after Spengel.)

c. Dorsal Tubular Central Nervous System.—The neural tube (brain and spinal cord) is dorsal to the notochord and arises by longitudinal infolding from the ectoderm of the mid-dorsal region. The system is truly tubular, with a central canal, or NEUROCŒLE. These two features of the central nervous system sharply distinguish that of the vertebrates from those of the various invertebrates; for in the latter the nervous system is usually ventral in position and solid. The earliest embryonic condition of the vertebrate central nervous system is the MEDULLARY PLATE stage, a thickened dorsal plate of ectoderm. As development proceeds, the margins of the elongated plate rise up to form the medullary folds, with a sort of gutter or groove running lengthwise between them—the MEDULLARY GROOVE. The folds arch toward each other and gradually come together in the mid-dorsal line, fusing to form a tube—the MEDULLARY TUBE. The tube breaks away from the contiguous ectoderm, the latter closes together above, and the central nervous system thus becomes an internal one. Regional specialization of the walls of the neural tube give rise to the various specialized subdivisions of the brain. Paired cranial and spinal nerves grow out segmentally from it to all parts of the body.

When we come to deal with the various divisions of the Chordata we shall examine their credentials to determine whether they have a right to membership in the Phylum Chordata.

B. THE SUBPHYLA OF CHORDATES

Because the various groups that are gathered together to form the Phylum Chordata consist of animals so extremely different from one another it is customary to separate them rather more definitely than if we were to call them merely classes; so they are divided into four subphyla.

Subphylum I. Hemichordata.—This group consists of the acorn worms and their microscopic relatives, *Cephalodiscus* and *Rhabdopleura.* A classic example of this group is *Balanoglossus* (Fig. 189). This animal has a body organization all its own. Its main parts are PROBOSCIS, COLLAR, and TRUNK, instead of the fa-

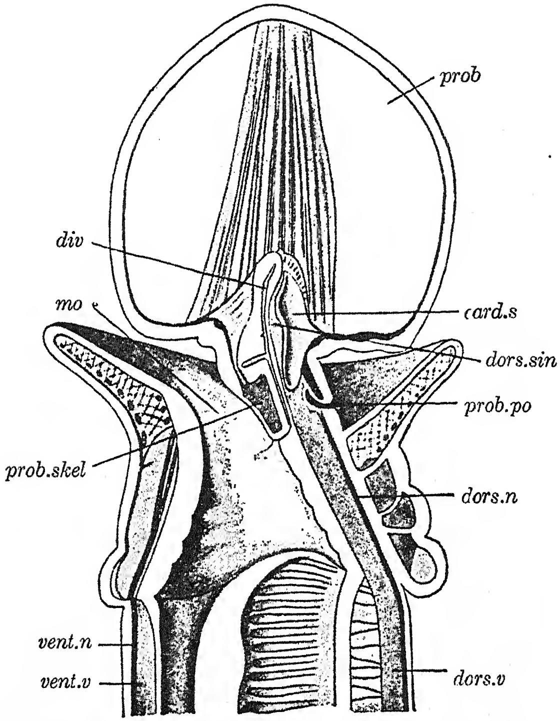


FIG. 190. *Balanoglossus.* Diagrammatic sagittal section of anterior end. *card. s,* cardiac sac; *div,* divericulum (supposed notochord); *dors. n,* dorsal nerve strand; *dors. sin,* dorsal sinus; *dors. v,* dorsal vessel; *mo,* mouth; *prob,* proboscis; *prob. po,* proboscis pore; *prob. skel,* proboscis skeleton; *vent. n,* ventral nerve strand; *vent. v,* ventral vessel. (From Parker and Haswell, after Spengel.)

miliar head, trunk, and tail of vertebrates. The proboscis and collar are hollow and filled with water; which is taken in and emptied through WATER PORES. The body plan is therefore hardly at all like that of typical chordates. Why then call Balanoglossus a chordate? In the first place, it has a little stiff process, the diverticulum, which grows out from the mid-dorsal part of the anterior

region of the digestive tract and protrudes forward into the proboscis (Fig. 190, *div*). It may or may not have a supporting function. This structure has been called a notochord, but this is a peculiar place for a notochord, for notochords usually run backward from the brain and lie beneath the nervous system. Many biologists seriously question whether this structure is really homologous with true notochords. Balanoglossus has plenty of gill slits, but whether they are really homologous with pharyngeal clefts, since they are in the trunk rather than in the head, is uncertain. There is said to be a dorsal tubular central nervous system (Fig. 190, *dors. n*), but what really exists is a region on the dorsal side of the collar that has rather more nerve cells than surrounding tissues and is for a short distance grooved lengthwise or even closed to form a short tube open at both ends. There is also a ventral nerve, which is certainly not a chordate characteristic. It seems highly questionable whether this peculiar nervous system is homologous with the central nervous system of vertebrates. Balanoglossus has a larval stage (TORNARIA LARVA) which is very much like the larvæ of echinoderms; also the water cavities and water-pores in proboscis and collar remind one a little of the water-

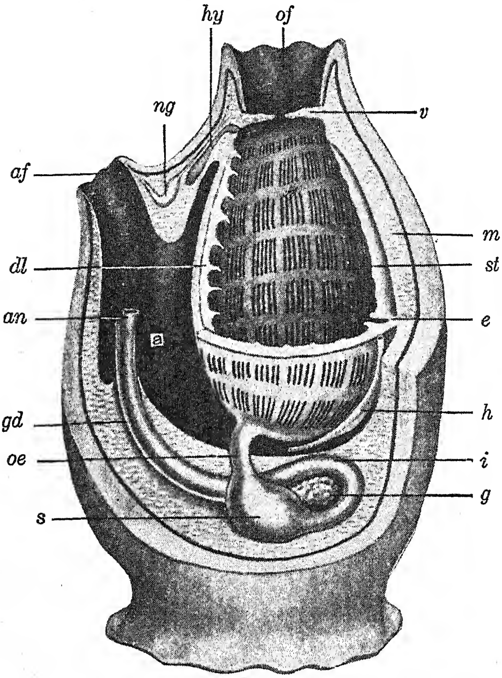


FIG. 191. Internal anatomy of a typical Ascidian. *a*, atrial cavity; *af*, atrial funnel or atriopore; *an*, anus; *dl*, dorsal lamina; *e*, endostyle; *g*, gonad; *gd*, duct of gonad; *h*, heart; *hy*, hypophyseal duct; *i*, intestine; *m*, mantle; *ng*, neural gland; *oe*, œsophagus; *of*, oral funnel or mouth; *s*, stomach; *st*, stigmata or subdivided pharyngeal clefts; *v*, velum. (Considerably modified after Hertwig.)

vascular system of echinoderms, since both are derived from cœlomic pouches. Perhaps the best we can say for Balanoglossus and its kin is that they seem to belong to the same general part of the phylogenetic tree as do chordates and echinoderms. That they are really chordates seems, to say the least, very doubtful. Hence we shall deal with them at no greater length.

Subphylum II. Urochordata.—This is a large and highly varied group of which we shall consider only the tunicates as the best known types. An adult tunicate (sea squirt) would almost surely be rejected if applying for admission to the chordates, for all it could show by way of credentials would be an enormous food sieve (Fig. 191), which is a pharynx provided with numerous

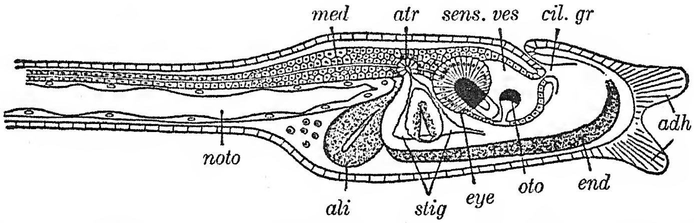


FIG. 192. Anterior end of the "tadpole" larva of an Ascidian (*Ascidia mammillata*) in optical section. *adh*, adhesive papillæ; *ali*, rudimentary alimentary tract; *atr*, atrial aperture; *cil. gr*, ciliated diverticulum, becoming ciliated funnel; *end*, endostyle; *eye*, eye; *med*, nerve-cord; *noto*, notochord; *oto*, otocyst; *sens. ves*, sense-vesicle (cavity of brain); *stig*, earliest stigmata or pharyngeal clefts. (From Parker and Haswell, after Kowalevsky.)

gill slits and an endostyle like that of Amphioxus, of which we shall soon speak. The adult tunicate has no notochord and no dorsal tubular nervous system. If it were not for its tadpole larva (Fig. 192) its claim to be considered a chordate would be very poor, but the larva makes good on the missing credentials, for it has a very good notochord and an even better brain and spinal cord than has Amphioxus, about whose chordate qualifications there is no question.

The life history of the tunicate is interesting. In its early embryonic stages it resembles Amphioxus, and it makes a very promising start to be an even better chordate than the latter. For some unknown reason, however, after being an active swimmer for some time, it settles on the bottom and attaches itself by suckers on its "chin," after which it undergoes regressive changes that involve the total resorption of the tail and its notochord, of most

of its dorsal surface, including its promising little brain of which only a vestige is left, and it finally becomes a stationary object that is little more than a living food bag. In spite of their degenerate adult condition, the tunicates and their relatives can hardly be excluded from the Phylum Chordata, since the larva is a pretty good chordate.

Subphylum III. Cephalochordata.—All the members of this group are small, somewhat fish-like creatures of which *Amphioxus* (*Branchiostoma*) is the type. Amphioxus looks something like a skinned sardine, for it is pink and somewhat translucent. It lives a double life, spending most of its time largely buried in the sand and feeding by the ciliary food-collecting mechanism common among invertebrates. From time to time it leaves its burrow and swims to a new location, where it burrows into the sand again by means of a swift vibratory action of the whole body produced by the segmented musculature of the body wall.

Its method of feeding is as follows: Water is sucked into the mouth, which can open or shut by relaxation or contraction of the circular muscles surrounding it, and is carried into the saclike pharynx. The latter is perforated by fifty or more diagonal gill slits, which are narrow enough to keep in the food particles but wide enough to allow water to pass through. On the floor of the pharynx is a glandular ciliated groove, the ENDOSTYLE (like that of the tunicates), which secretes a sticky mucous rope. This acts like a moving fly paper, catching the microörganisms that are forced down upon it by the cilia lining the pharynx. This mucous rope travels first forward, goes round the mouth, and then is carried along a dorsal groove back to the stomach-intestine where the food is digested. It is in the details of this complex feeding and respiratory mechanism that Amphioxus, tunicates, and the larvæ of the lowest vertebrates (lampreys) most definitely correspond.

Anatomically, Amphioxus, as seen in the illustration (Fig. 193), has a notochord running from end to end of the body. It has a tubular central nervous system dorsal to the notochord, but the brain is very degenerate, so much so that most authors describe Amphioxus as acephalic, or headless. With regard to the three main requirements for a chordate, therefore, Amphioxus has no difficulty in passing muster.

Without going into minor details, it should be said that the

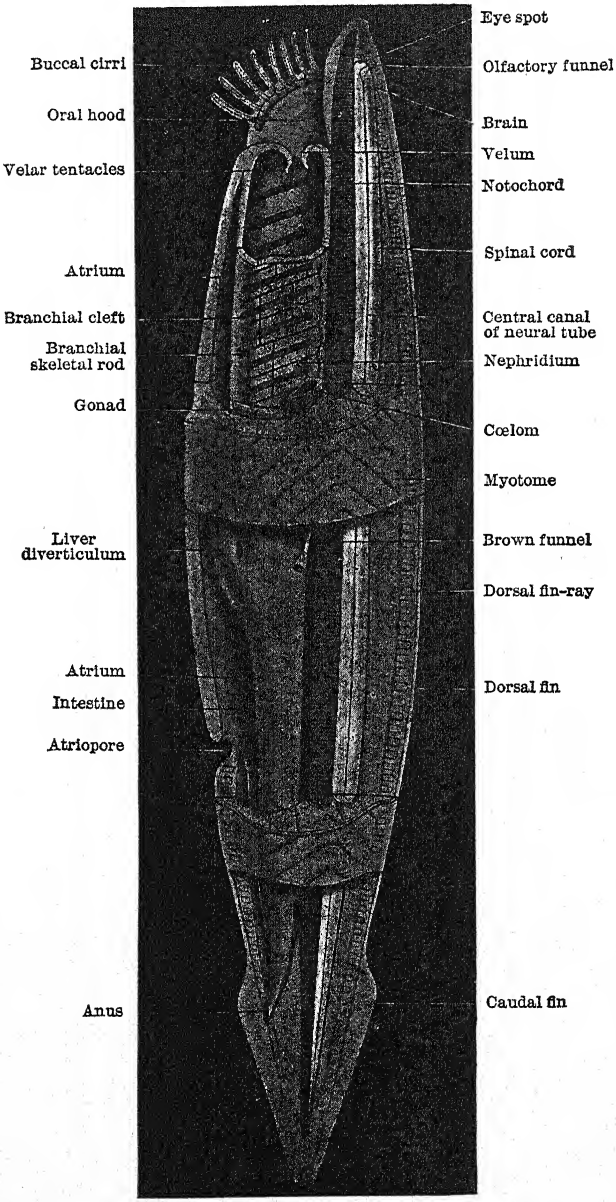


FIG. 193. General anatomy of Amphioxus. (Redrawn after Parker and Haswell.)

digestive tract is straight, not coiled, as in vertebrates; there is no specialized heart, but only a pulsating ventral vein with valves; paired NEPHRIDIA which are cœlomoducts; an ATRIUM and ATRIOPORE, which is anatomically an extra fold of the body wall and which serves as an adaptation for sessile life; a rather poorly developed MEDIAN FIN SYSTEM supported by short connective tissue rays; eggs that are microscopic and possess little yolk; and a developmental history that involves a diagrammatic cleavage plan, a hollow blastula and a typical free-swimming gastrula stage. Many other anatomical and embryological details are omitted for the sake of brevity.

Subphylum IV. Vertebrata (Craniata).—In this place we shall not attempt to characterize the vertebrates further than we have already done in the synoptic classification in Chapter XIII. Nor shall we go any further into a classification of the group. This is a course in General Zoölogy and does not contemplate including the materials of courses in Vertebrate Zoölogy. In the several chapters following this the frog is dealt with as a type vertebrate and its anatomy, physiology, embryology, and behavior are presented in some detail.

Before proceeding to the special biology of the frog as a vertebrate type we shall present a sketchy story of the evolutionary history of the chordate phylum, especially that of the vertebrates. In this group the fossil evidences are perhaps more adequate than in any other phylum and this permits of more definite statements than could otherwise be made. It is impossible here to document the story by a catalog of evidences, but biologists regard the evidences as adequate.

C. Evolutionary History of Chordates

The earliest ancestors of the chordates are unknown, for there are no fossil representatives of them. They are believed to have been small, soft-bodied creatures possibly resembling the larvae of Balanoglossus and the echinoderms. The immediate ancestors of the vertebrates and probably also of the tunicates were probably somewhat like Amphioxus, but certainly must have had better brains than the latter and probably had not developed the specialized mechanisms for sedentary feeding which characterize Amphioxus and the tunicates. From such an ancestral type it seems reasonable to believe that the true vertebrate ancestor

branched off and became specialized for a free-swimming life, while another branch of the same ancestral stock gave rise to Amphioxus and the tunicates, which became partially or wholly degenerate in connection with sedentary habits.

The earliest true vertebrates of which we have a fossil record were the OSTRACODERMS (Fig. 194), a group of armored fish-like

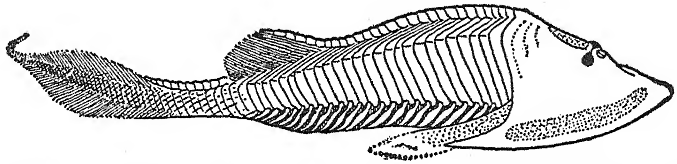


FIG. 194. *Cephalaspis*, an extinct jawless, limbless vertebrate—an Ostracoderm. (After Patten.)

animals that throve and became extinct in the Silurian (nearly 400,000,000 years ago). They were JAWLESS and LIMBLESS, and in this respect more primitive than the true fishes that came later. Modern representatives of this level of vertebrate evolution are the LAMPREYS (Fig. 195) and HAGFISHES, which are regarded as

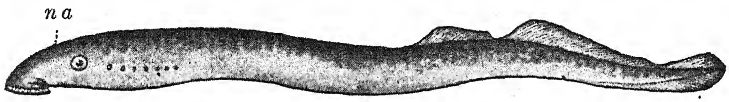


FIG. 195. *Petromyzon* (Lamprey), a present-day survivor of the jawless, limbless vertebrates. *n a*, position of single, median nostril. (After Parker and Haswell.)

specialized and somewhat degenerate descendants of the same stock to which the Ostracoderms belong.

From some branch of the jawless and limbless vertebrates arose the first TRUE FISHES, which became abundant in the Devonian period (some 40,000,000 years later). These fishes acquired JAWS and PAIRED LIMBS (fins), which characterize all higher vertebrate groups. The jaws seem to have been derived through modification of the skeletal elements of the first gill arch, while the paired fins seem to be regional specializations of an earlier continuous pair of fin folds. One branch of the early fishes (CHONDRICHTHYES) had a cartilaginous skeleton and gave rise to the modern sharks (Fig. 196) and their relatives; the other branch (OSTEICHTHYES) were the PRIMITIVE BONY FISHES. The Chondrichthyes, at first river dwellers, later became marine, while the Osteichthyes are regarded as having been originally inhabitants of rivers

and lakes. As their name indicates, they have a bony skeleton. In addition, they also possessed PRIMITIVE LUNGS as well as gills, so that they could breathe air when the water became stagnant or

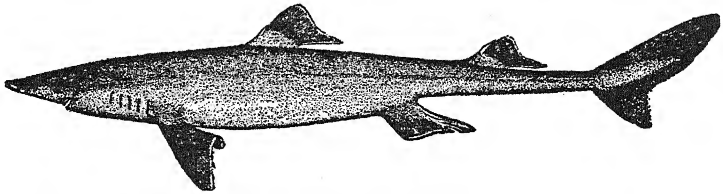


FIG. 196. *Squalus acanthias*, the dogfish shark, a good example of modern Chondrichthyes. (From Hegner, after Dean.)

scarce. One of the several branches of these primitive bony fishes was that of the LOBE-FINNED FISHES, which inhabited temporary ponds and swamps. They had fairly good lungs and, what is even more important, incipient legs. Each paired fin had a projecting

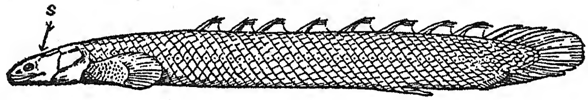


FIG. 197. *Polypterus*, the most primitive surviving ray-finned fish, resembling extinct lobe-fins. *s*, position of spiracle. Note the fleshy lobes of the front fins. (After Traquair.)

fleshy lobe at its base, a lobe with a skeleton comparable with the limb skeleton of land vertebrates. Modern descendants of this group are the lung-fishes of Australia and Africa, ray-finned fishes (Fig. 197), and the Amphibia.

From the lobe-finned fishes arose the PRIMITIVE AMPHIBIA, which at first were not very different from their fish ancestors (Fig. 198). They were semiaquatic forms, which had merely developed better lungs and better limbs than their ancestors. Some of our modern Amphibia, such as the hellbender and newts are not so very different from the early Amphibia. The modern frogs and toads, however, represent a highly specialized side line of amphibian evolution. The first amphibian fossils are found in the Upper Devonian, not long after the first specialization of lobe-finned fishes. The Amphibia never succeeded in adapting themselves at all fully to terrestrial life. They had to stay close to the

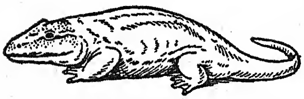


FIG. 198. *Eryops*, a good example of the earliest Amphibia. (After Osborn.)

water, for they laid their eggs in the water and the larval stages, tadpoles, required a water habitat. Even today the Amphibia are mainly semiaquatic, only a few tree toads having acquired adaptations that relieve them of the necessity of seeking the water to breed.

From a very primitive amphibian group, not long after the Amphibia had become established as the first invaders of the dry land, arose the PRIMITIVE REPTILES (Fig. 199). These introduced a novel and very important adaptation for land life, the so-called "land egg." The term "land egg" includes the characteristic embryonic membranes amnion and allantois, which will not be discussed here. The egg during its passage down the oviduct becomes coated with a thick layer of food albumen, and with a tough protective shell that prevents desiccation but permits an exchange of metabolic gases. The large store of food in the form of yolk and the layer of albumen permits the young to develop up to an advanced stage before hatching. After hatching, therefore, they are self-sufficient and able to take care of themselves and get

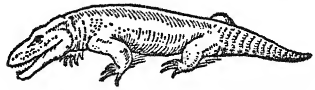


FIG. 199. *Seymouria*, an example of the earliest and most primitive reptiles. (After Osborn.)

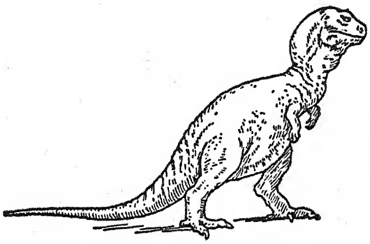


FIG. 200. *Tyrannosaurus*, a giant carnivorous dinosaur of the Mesozoic. (After Osborn.)

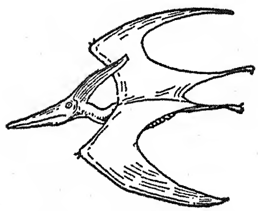


FIG. 201. A pterosaur, a type of flying reptile of the Mesozoic. (After Osborn.)

their own food. This invention of the land egg gave the reptiles a tremendous advantage over the Amphibia and led to their domination of the land, a domination that lasted for over a hundred million years. During the entire age of reptiles (the Mesozoic) the world was peopled by the so-called RULING REPTILES, including the dinosaurs (Fig. 200) and the pterosaurs (Fig. 201). Few chapters in the history of animal life are so dramatic as that of the dynasty of the dinosaurs. Some of these remained small

and inconspicuous, but others grew to giant size. Tempting as it is to elaborate upon the golden age of the reptiles we must refrain.

Apart from giving rise to the modern reptiles, lizards, snakes, turtles, and crocodiles, the reptiles gave off two special branches that developed into the birds and the mammals.

Birds seem to have arisen from an early type of small bipedal dinosaur. Two genera of fossil primitive birds, of which *Archæopteryx* is the classic example (Fig. 202), are almost entirely reptilian in their characters, but also had feathers and wings. The further evolution of birds has given rise to running birds such as the ostrich and to a vast assemblage of feathered folk, that play such a conspicuous part in our natural scheme.

Fig. 202. The "bird-lizard," *Archæopteryx*. (After Heilmann.)

Mammals got their start much earlier than birds, but were unable to make very rapid progress until the contemporaneous ruling reptiles had become extinct. No doubt the birds, on account of their powers of flight, had a better chance during the Mesozoic, but even they were doubtless held back by the Pterosaurs (flying Ruling Reptiles). Even before the reptiles had entered upon their great career of success, one branch of primitive reptiles, the mammal-like reptiles, had begun to experiment with mammalian characteristics. Abundant fossil remains of this early reptilian group show that these animals had already started to become mammals, some types developing one mammalian feature, other types others. But no one type had gone all the way. In this rather tentative mammalian condition the reptile ancestors of the mammals lived on into the Age of Reptiles. Some of them developed into true mammals, but these were small and inconspicuous and did not compete successfully with the great reptiles with whom they lived. But their time came when, at the close of the Age of Reptiles, all the dominant reptilian groups became extinct. This left the land wide open for any ambitious group to take possession of. The birds and mammals had about equal chances, but the mammals took advantage of it more successfully in some important respects than did the birds. The birds specialized as flying mechanisms, but the mammals went in for intel-

ligence. From an early period the mammals developed larger and better brains and it is due to this line of specialization that one branch of the mammals, the primates, to which man belongs, attained its supremacy. The mammals of today belong to nearly a score of orders, conspicuous among which are the insect-eaters, the rodents, the bats, the carnivores, the odd-toed hoofed animals, the even-toed hoofed animals, the sea cows, the whales, and the primates.

The PRIMATES are believed to have arisen from a primitive branch of the mammalian order, Insectora (Fig. 203). The earliest

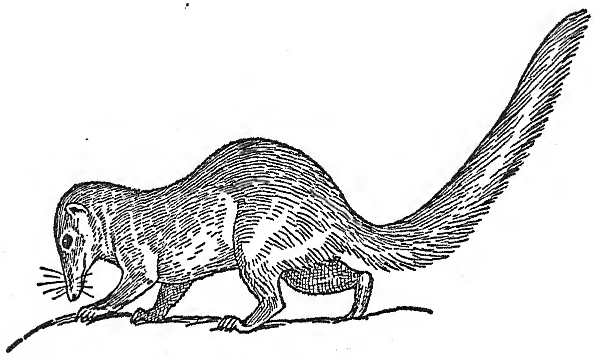


FIG. 203. *Tupaia*, the tree shrew, regarded as the most primitive of modern placental mammals. From some such type as this the primates seem to have originated. (After Osborn.)

primates seem to have been arboreal and were possibly somewhat like the present-day lemurs. Later appeared a group somewhat like South American monkeys. Still later came a group not unlike Old World monkeys (baboons, etc.), and after them appeared the anthropoid apes, somewhat like the present gorillas, chimpanzees, orang-outangs, etc. And finally, latest of all, appeared primitive man. All the living lower primates may be regarded as side lines of evolution that branched off from the human ancestral tree millions of years ago. Both they and man have diverged from the ancestral stocks and each has specialized along different lines. None of the existing primates is, therefore, ancestral to man.

The pre-history of man is to be read in a series of fossil remains and in artifacts left by early man. The first fossil remains of a human type are those of the ape-man, *Pithecanthropus erectus*, a small-brained, low-browed fellow, with many primitive charac-

ters intermediate between those of modern man and modern apes. *Sinanthropus*, perhaps the next oldest human type, though most recently discovered, represents a step higher in the scale, and the *Piltdown man* and *Neanderthal man* still further steps upward. While the fossil story of primitive man is far from complete, it now seems clear that man rose from a generalized stock of primitive anthropoids that divided over a million years ago into a human branch and an anthropoid-ape branch. Each of these branches has followed a long road of specialization, but in different directions, so that at present they are farther apart than at any previous period. As we trace back from the present the fossil pedigrees of these two branches we find the human types becoming less distinctly human and perhaps more ape-like, while the ape types become less ape-like and a little more human. Pithecanthropus seems to be a human type that developed shortly after the main human branch diverged from that of the apes.

The rest of the story of human evolution would involve a consideration of present-day races of man, their origins and interrelations. This specialized field of anthropology is beyond the range of the subject matter of a course in zoölogy.

SUMMARY

1. The Phylum Chordata is very heterogeneous.
2. The three fundamental characteristics of the phylum are: notochord, gill slits, and dorsal tubular nerve cord.
3. The Subphylum Hemichordata, including Balanoglossus and relatives, is a group of uncertain affinities. While there is a good deal of doubt as to whether these animals possess a real notochord and a real dorsal tubular nerve cord, they are believed to be at least more nearly related to chordates and echinoderms than to any other phyla.
4. The Subphylum Urochordata (tunicates, etc.) are regarded as sessile, degenerate descendants of an early true chordate ancestor. In the larval stage the notochord is present and the nervous system is typically chordate. In the adult only the gill slits and the food concentrating mechanism suggest their chordate affinities.
5. The Subphylum Cephalochordata (Amphioxus) has all chordate characters almost diagrammatically shown. Apart from the degenerate brain and head, Amphioxus would be a fairly good replica of the probable ancestor of the vertebrates.
6. The Subphylum Vertebrata (Craniata) comprises the true vertebrate chordates, consisting of cyclostomes, fishes, amphibians, reptiles, birds, and mammals.
7. A brief story of the evolutionary history of the vertebrates emphasizes the following main milestones in a progressive upward journey:

a. The unknown ancestor probably was soft bodied, possibly rather like Amphioxus.
b. The earliest vertebrates were aquatic forms without jaws or paired limbs.
c. The addition of jaws and limbs constitutes the first great advance at the fish level.
d. Some of the primitive bony fishes had swim-bladder lungs and paired fins with fleshy lobes.
e. From some of these lobe-finned fishes came the first Amphibia.
f. Some of the earliest amphibians invented the "land egg," with amnion and allantois, and these became the first reptiles.
g. Among the early reptiles was a group of mammal-like reptiles, which slowly but surely evolved into mammals.
h. The main groups of reptiles went on to give rise to the Ruling Reptiles of the Age of Reptiles.
i. From an early group of Ruling Reptiles, the bird-like dinosaurs, arose the true birds.
j. The mammals were inconspicuous during the Age of Reptiles, but after the extinction of most of the great reptile orders they took possession of the earth and have ruled it up to the present.
k. The primates, the group to which man belongs, seem to have arisen from a primitive group of arboreal insectivores. The main characteristics of Primates seem to have evolved in connection with arboreal life involving erect posture and bifocal vision.
l. The earliest fossil remains of man indicate that man and the anthropoid apes were derived from a common ancestor that lived over a million years ago.

CHAPTER XXXII

THE FROG: TAXONOMIC POSITION AND ACTIVITIES

THE frog is used extensively the world over as a laboratory animal. The reasons for its popularity are not far to seek. Frogs are of very wide occurrence; they are of convenient size; they are easily kept alive for long periods; they stand near the middle of the vertebrate series, exhibiting both aquatic and terrestrial adaptations; their eggs are easily obtained and their embryogeny easily studied; and, finally, it has come to be a time-honored custom to use the frog either as an introductory type or to place it at the end of an evolutionary series and to make it the object of intensive study. In one large university with which the writer was connected there was a so-called "Frog Course," which occupied the second semester of the first year course in Zoölogy. This section of the present text, dealing as it does more or less intensively with the frog, is so designed that it will be found equally available as an introduction to the study of animal types or as the last one of a series of animals representing various levels of increasing complexity of organization.

A. THE FROG'S PLACE IN NATURE

Frogs belong to the PHYLUM CHORDATA and the SUBPHYLUM CRANIATA (VERTEBRATES). There are seven classes of Vertebrates:—

Class 1, **Cyclostomata**—lampreys and hagfishes.
Class 2, **Chondrichthyes**—sharks and skates.
Class 3, **Osteichthyes**—bony fishes.
Class 4, **Amphibia**—newts, salamanders, and frogs.
Class 5, **Reptilia**—lizards, snakes, turtles, alligators.
Class 6, **Aves**—birds.
Class 7, **Mammalia**—mammals (beasts, quadrupeds).

According to this classification, there are three thoroughly aquatic classes, three thoroughly terrestrial classes, and one am-

phibious class, neither fully aquatic nor fully terrestrial, the Amphibia. The Amphibia constitute a sort of transitional group, some of which are aquatic through life, though having lungs as well as gills; others are thoroughly aquatic during their embryonic and larval periods, but are more or less terrestrial in the adult stages. The frog belongs to the latter category.

The Frog as an Amphibian

As we have just seen in the list of vertebrate classes given above, the Class Amphibia was placed in a central position; for they are considered representative of the vertebrates as a whole. The principal characteristics of the Amphibia and the ways in which this class differ from other vertebrates follow:—

(1) The limbs are of the five-fingered or hand type, characteristic of terrestrial as opposed to aquatic vertebrates.

(2) The heart has two auricles and one ventricle. It is three chambered, and in this way is transitional between the two-chambered heart of the fishes and the four-chambered heart of the birds and mammals.

(3) Functional gills are present at least during the larval period.

(4) The cranium is articulated with the ATLAS—the terminal vertebra of the neck—by means of two rounded pivots, the OCCIPITAL CONDYLES.

(5) There are no scales in modern Amphibia, except in the Apoda, where minute dermal scales are imbedded in the skin.

(6) The teeth of modern Amphibia are small and inconspicuous.

(7) The eggs develop (with some exceptions) in water, and do not have an AMNION nor an ALLANTOIS, embryonic membranes of great importance in the embryonic life of terrestrial vertebrates.

The CLASS AMPHIBIA, so far as living types are concerned, is divided into three orders:—

Order 1, Apoda—characterized by the lack of both legs and tail during the adult period. Example, cæcilians or blind worms.

Order 2, Urodela—characterized by the possession of both legs and tail during the adult period. Example, salamanders.

Order 3, Anura—characterized by the possession of legs and by the lack of a tail during the adult period. Example, frogs.

The ORDER ANURA is divided into two suborders:—

Suborder 1, Aglossa—characterized by the absence of a tongue. This is a small group represented by the Surinam Toad (*Pipa americana*). (See Fig. 241.)

Suborder 2, Phaneroglossa—characterized by the presence of a tongue. This group contains nearly all of the frogs and toads.

Most of the common frogs belong to the FAMILY RANIDÆ and to the genus RANA.

B. ACTIVITIES OF THE FROG

1. *Habitat*

Most of the true frogs of the genus Rana are aquatic or at least semiaquatic. One expects to find them either actually in the water, as is the case with the bullfrog (*Rana catesbiana*), or else along the shores of streams, ponds, or lakes, as in the case of the grass frog or leopard frog (*Rana pipiens*). Here they occupy a strategic position, being able to jump into the water to escape enemies on land or to climb out of water and hop away to escape aquatic enemies. Most of what we shall have to say in this section will have reference especially to *Rana pipiens*, the commonest of all North American frogs.

2. *Feeding Habits*

Frogs are carnivorous. Their favorite food consists of insects, worms, small fishes, and the young of their own or allied species. Earthworms seem to be especially relished by frogs, a liking shared by many other animals. Frogs are greedy feeders and are not very choice in their selection of food. Like many other animals, when food is plentiful, they stuff until they can hold no more. In catching insects or other swift moving prey the frog uses its tongue in a surprisingly facile manner. The tongue is hinged at the front of the lower jaw and may be suddenly flipped out so as to bat down a fly. A sticky secretion on the end of the tongue enables the latter to hold small insects till they can be flipped back into the mouth (Fig. 204). The tongue is shot out by means of a curious mechanism: a large lymph sac beneath the tongue fills suddenly, lifting and throwing forward the free end of the tongue. Contraction of the lingual muscles flips it back into the mouth.

3. *Jumping and Swimming*

The frog is an athlete of considerable versatility: an expert broad jumper and an exceptional swimmer and diver. His chief assets in both terrestrial and aquatic locomotion are his highly developed hind legs. When resting on land, the hind legs are always flexed in readiness to jump, the forelegs acting merely to support the front end of the body and to change the direction of the leap. In swimming, both hind legs are folded forward into the shape of a Z and then straightened, the great webbed foot being shoved broadside on against the water. This is not at all like the so-called "frog stroke" used by human swimmers; for in that stroke the propulsion is secured by forcing the water backward between the thighs. The forelegs of the frog are of little use in swimming, being mainly used for guiding purposes. In diving, we distinguish two quite different operations. The first is a leap from the land into the water, a headfirst plunge executed with much neatness; the second is a vigorous swim to the bottom. Usually when jumping from the shore, the frog, even before reaching the bottom, makes a quick shoreward turn and buries himself in the mud. When the frog is resting on the surface, diving is a more complicated operation. The first step is a sudden withdrawal from the surface, accomplished by a quick forward stroke of the hind legs. The second step, as before, consists of a swim to the bottom. Frogs rest in the water by floating. The position when floating is one in which the legs are fully extended, while the nostrils and eyes are the only parts of the body above the surface. One sees here the advantage of having the eyes set high on top of the head. The extended position of the hind legs is one that spells readiness for quick withdrawal from the surface, when a fraction of a second may mean either safety or peril.

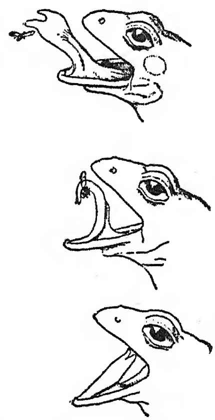


FIG. 204. Three stages of the movement of the tongue of a frog, *Rana esculenta*. (From the Cambridge Natural History.)

4. *How the Frog Croaks*

Some writers have attempted to spell out the syllables of the frog's spoken language, but with indifferent success. The most

feasible spelling seems to be "au-au-au-auk," but even this bears not the slightest resemblance to what the frog actually says. Most people know what he says, though they are unable to spell it. The males are the chief croakers and seem to be proud of their superiority in this respect, especially during the breeding season, when the voice of the male seems to charm and captivate the female. The vocal organ of the frog consists of vocal cords. Air is forced out of the lungs over the cords into the mouth. The sound is amplified by means of vocal sacs, which are inflated portions of the mouth and pharynx. Both nostrils and mouth are kept closed so that the buccal cavity is distended. This then contracts and forces the air back over the cords into the lungs. Thus a series of croaks may be made without taking breath; and hence the frog can croak under water. The vocabulary of the frog, though limited, is sufficiently varied to express the ordinary gamut of emotions: a low grunt indicating contentment, a sharp cry or scream when in pain or peril, and various modulated croakings when engaged in courtship.

5. *Why the Frog Swells Up*

We have all heard the fable of the frog who tried to inflate himself so as to rival the ox in size. While not being able to vouch for the motive thus imputed, we do know that there are times when the frog finds it advantageous to make a balloon of himself. When seized by a snake or other enemy, he fills himself with air and thus becomes round and slippery, a difficult object to swallow.

6. *Enemies of the Frog*

Apart from their agility both on land and in the water, and their excellent protective coloration, frogs are almost entirely defenseless and fall an easy prey to many predaceous animals. Perhaps their worst enemy is man, who desires the hind legs for food and uses millions of specimens a year for laboratory purposes. Other frog eaters are snakes, herons and their kind, crows, skunks, water rats, and turtles. Various species of water bugs and leeches catch tadpoles and suck their blood. Beside this type of enemy, the frog has numerous parasites. Various species of nematodes or roundworms infest the lungs and other organs. Flukes of several kinds are inhabitants of intestines, lungs, and bladder. Protozoan parasites, chiefly belonging to the Class Sporozoa, are numerous.

Especially noteworthy is the parasitic ciliate, *Opalina*, found in the frog's intestine. With all of these enemies, outside and inside, it seems a wonder that the poor frog survives at all. It is only its ability to reproduce immense numbers of offspring that saves the race from extinction, for only one in hundreds survives to adult life.

7. *Seasonal Changes*

In early SUMMER the frog is thin and hungry and spends most of his time feeding. When fat and satiated, he retires to sheltered places, spending the midsummer season in what has been called somewhat erroneously the "summer sleep"; for it is only a period of relative inactivity and easy living. In the AUTUMN of the year the frog is fat and well nourished, with much reserve food for the hard winter. Besides accumulations of fat, much reserve food is stored in the liver, in muscles, and elsewhere. In the late fall frogs go into WINTER quarters. There they hibernate. In doing so they retire below the frost line at the bottom of ponds or streams, bury themselves in the mud and remain dormant till the spring, carrying on the various functions only at their lowest possible levels. There is so little metabolic activity that oxygen enough is obtained through the mud covered skin to satisfy all requirements. The reserve food supply is used up partly for fuel to keep the spark of life smoldering and partly for elaborating the sexual products, which grow during the winter at the expense of other tissues. In the SPRING, when the frog first wakes up from the winter sleep, the most active tissues of the body are the reproductive organs, and these control the activities until their demands are satisfied. Even hunger must await its turn for satisfaction. The breeding habits demand separate consideration.

8. *Breeding Habits*

The male frog has an uncontrollable obsession to clasp something, preferably a female frog, with its forelegs. Once the arms are clasped about the female's body, thumbs locked together, the male is very difficult to dislodge. He is in a sort of trance. Even cutting him in two seems to have little effect on him, for he will continue to clasp until loss of blood weakens him and his grip is loosened. The value of this reflex on the part of the male is that it insures fertilization of the eggs; for eggs are laid only after the

male has clasped the female for some days. When the female is ready to extrude the eggs, the pair sink together to the bottom. As the eggs emerge from the genital opening, the male discharges spermatic fluid over them, and fertilization takes place in a very high percentage of the eggs. After the entire batch of eggs is laid and forms a gelatinous mass, the male loosens his clasp, and from then on for the rest of the summer is totally indifferent to females. Sometimes, however, a female, after laying her first batch of eggs, may be clasped by a second male, in which event she is likely to bring to maturity and lay a second batch of eggs. The development of the frog is to be dealt with in detail in a subsequent chapter.

9. *Hypnosis*

One may readily hypnotize a frog. If seized in the hands and held gently but firmly on its back till it ceases to struggle, it will usually remain motionless for some time. The position taken by the limbs during hypnosis is said by ***Verworn*** to be equivalent to that assumed by a frog performing righting movements—movements normally performed when the animal is inverted. The muscles are believed to be in a state of tonic contraction. The heartbeat and breathing movements, at first more rapid than normal, soon settle down to a rhythm much slower than normal. Any sudden stimulus serves to awaken the frog from the state of hypnosis; while absolute quiet and lack of visual and tactual stimulation may induce a very protracted hypnosis, lasting for hours.

Now that we have introduced the frog as a living organism operating as a unit, we may profitably turn our attention to the details of the organic machine.

SUMMARY

1. Frogs belong to the Phylum Chordata, Subphylum Vertebrata (Craniata), Class Amphibia, and Order Anura, a group chiefly characterized by lack of tail in the adult state.
2. Amphibia differ from fishes in having: feet with five digits instead of paired fins; the heart three-chambered (two auricles and one ventricle); lungs well-developed; an external ear opening with ear drum; etc.
3. Amphibia differ from reptiles, birds, and mammals in having a "water egg" (without amnion and allantois), gills are present at least in the larvæ, etc.
4. The Class Amphibia has the following surviving orders: Apoda (the burrowing limbless, tailless cæcilians); Urodela (the newts and salamanders, with tails in adults); and the Anura (with tailed larvæ and tailless adults).

CHAPTER XXXIII

ANATOMY OF THE FROG

THE following somewhat dry account of the anatomy of the frog may seem superfluous to those students who make a thorough laboratory study of this animal, but teachers demand the data here presented for review purposes and for other reasons.

A. GROSS ANATOMY

a. External Features.—The following structures are easily noted: *a*, the paired nostrils, or EXTERNAL NARES; *b*, the paired eyes with two eyelids, the upper almost immovable, the lower a transparent movable membrane capable of covering the eye; *c*, the circular TYMPANIC MEMBRANES, or eardrums, just back of the eyes; *d*, the opening of the CLOACA on the dorsal surface between the hind legs; *e*, the two quite unequally developed pairs of limbs. The fore limb consists of UPPER ARM, FOREARM, WRIST, and HAND with but four DIGITS—the thumb being reduced to a tiny rudiment; the hind limb consists of THIGH, SHANK, and FOOT, with a long ANKLE region and five webbed digits, the shortest of which is the HALLUX, homologous with the human "great toe."

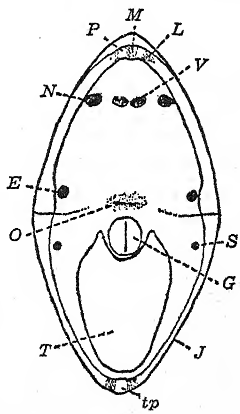


FIG. 205. Mouth of the frog widely opened. *E*, Eustachian tubes; *G*, glottis; *J*, lower jaw; *L*, lateral subrostral fossa; *M*, median subrostral fossa; *N*, posterior nares; *O*, œsophagus; *P*, pulvinar rostrale; *S*, opening of vocal sac; *T*, tongue; *V*, vomer; *tp*, tuberculum prelinguale. (From Holmes.)

b. Mouth Cavity.—A study of the mouth cavity shows a set of small teeth in the upper jaw, a set of VOMERINE TEETH in the roof of the mouth, INTERNAL NARES opening beside the latter, a pair of EUSTACHIAN TUBE openings near the angle of the jaws, the TONGUE hinged in front of the lower jaw, the GLOTTIS, or entrance to the lungs, and the GULLET (Fig. 205).

c. Body Wall.—The wall of the body is composed of the skin, body muscles, LYMPH SPACES, blood vessels, LIMB GIRDLES, and the PLEUROPERITONEUM, or lining of the body cavity. The skin is composed of a thin layer of SQUAMOUS EPITHELIUM on the outside (the EPIDERMIS) and a thicker internal layer (the DERMIS) composed of connective tissue, blood vessels, and glands. Near the surface one always sees parts of the INTERNAL SKELETON, especially the skull and the limb girdles. The lateral and ventral walls of the body are supported only by muscle layers. Several

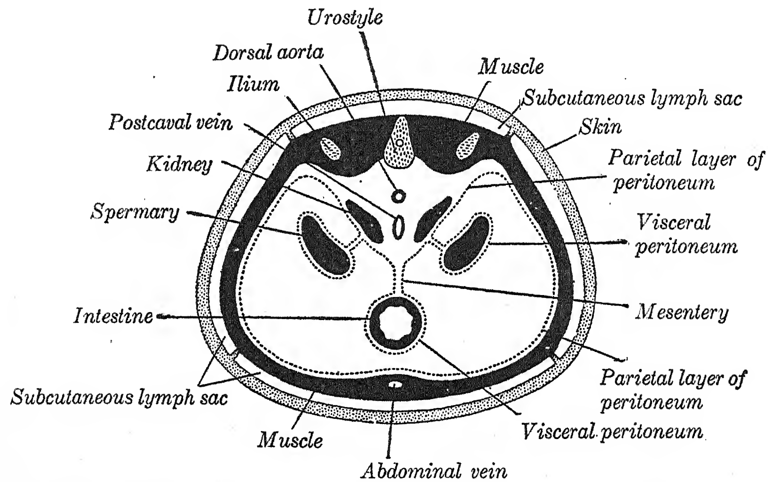


FIG. 206. Diagram of a cross section of the body of a frog showing the course of the peritoneum by a dotted line. (Redrawn after Parker and Parker.)

layers of these muscles deserve special mention: the paired RECTUS EXTERNUS muscles on the sides, the RECTUS ABDOMINIS along the median ventral region, and the PECTORAL muscles covering the ventral side of the upper body region.

d. Cœlom and Mesenteries.—The cœlom, or body cavity, is the large space within the body wall that contains the VISCERA. The viscera consist of: the ALIMENTARY TRACT and its derivatives—lungs, liver, pancreas; the circulatory system, including the heart and the chief arteries and veins; the lymph vessels; the excretory and reproductive systems; the sympathetic nervous system and the branches of the central nervous system innervating the viscera. The PERITONEUM lines not only the body wall but is wrapped about all of the visceral organs. The whole peritoneum, however,

remains a continuous sheet and extends from the body wall in the form of thin folds, the MESENTERIES, that serve to suspend and to protect the viscera. Each mesentery consists of a double layer, owing to the way in which the membrane enwraps the viscera. It is as though the wrapping of several articles were done by folding each up in a part of an elastic sheet, the edges of which were fastened to a wall. Each visceral organ thus comes to be wrapped in a sheet of tissue. The special sac of peritoneum loosely enwrapping the heart is known as the PERICARDIUM. The general relations of the body cavity and mesenteries are shown in the accompanying illustration (Fig. 206).

B. Special Anatomy

1. *The Skeletal System*

Most vertebrates have both an exoskeleton and an endoskeleton. The exoskeleton, sometimes known as the integument, appears in other animals in the form of scales, feathers, hair, bony plates, spines, but in the frog there is no superficial exoskeleton, the body being covered by a smooth, soft skin. Some of the ancestral integumentary elements, so-called dermal bones, have sunk beneath the surface and have become parts of the skull, limb girdles, and other parts of the internal skeleton.

The skeleton of the frog (Fig. 207) consists of an AXIAL SKELETON and an APPENDICULAR SKELETON, both made up of a complex of bones and cartilages. The axial skeleton consists of the SKULL, or CRANIUM, and the SPINAL COLUMN of vertebræ. The appendicular skeleton consists of the framework of the paired limbs and their supports, the PECTORAL and the PELVIC GIRDLES.

a. The Axial Skeleton.—The VERTEBRAL COLUMN comprises nine vertebræ and a long, slender posterior rod, the UROSTYLE. Each vertebra is a complex bony ring (Fig. 207) surrounding a part of the spinal cord. The thickened ventral part is known as the CENTRUM; the dorsal projection is called the NEURAL SPINE; the lateral riblike processes are termed TRANSVERSE PROCESSES; the other processes are called ZYGOPOPHYSES.

The SKULL and the VISCERAL SKELETON are shown in the accompanying illustration (Fig. 208). According to a generally accepted theory, the upper and lower jaws, together with the hyoid and laryngeal cartilages, were originally branchial arches,

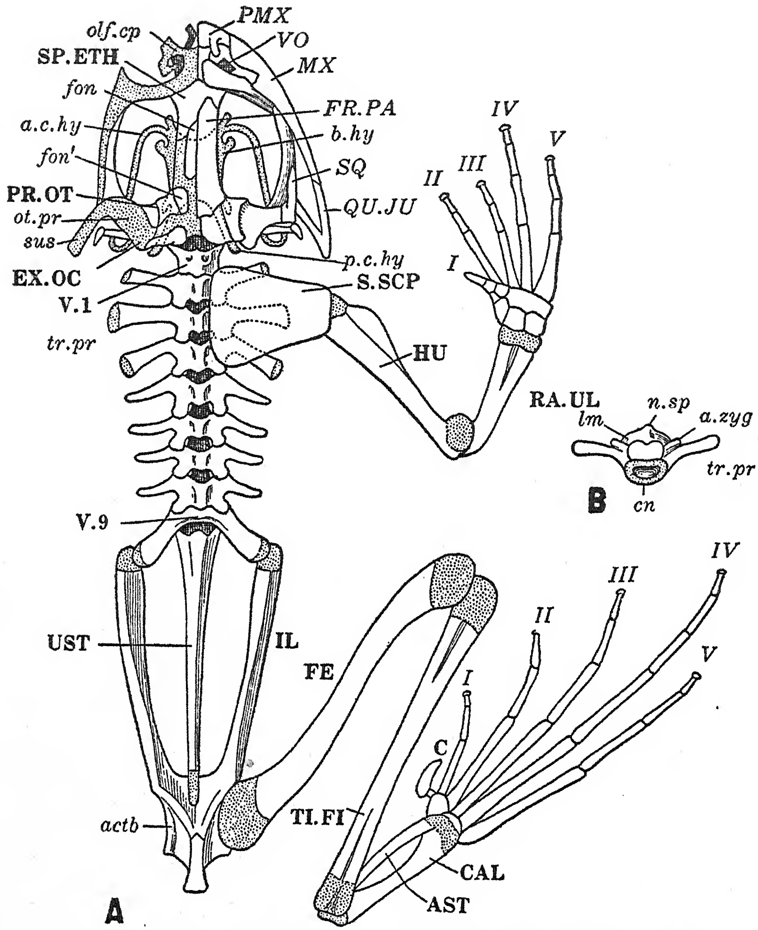


FIG. 207. A, skeleton of *Rana temporaria*. The left limbs, left shoulder girdle, and the membrane bones of the left side of the skull are removed. Cartilaginous parts dotted; names of cartilage bones in bold; those of membrane bones in italic capitals. *a.c.hy*, anterior cornu of hyoid; *actb*, acetabulum; **AST**, astragulus; *b.hy*, basi-hyal; **C**, calcar; **CAL**, calcaneum; **EX.OC**, exoccipital; **FE**, femur; *fon*, *fon'*, fontanelles; *FR.PA*, fronto-parietals; **HU**, humerus; **IL**, ilium; *MX*, maxilla; *olf.cp*, olfactory capsule; *ot.pr*, otic process; *p.c.hy*, posterior cornu of hyoid; *PMX*, premaxilla; **PR.OT**, proötic; *QU.JU*, quadratojugal; **RA.UL**, radio-ulna; **SP.ETH**, sphenethmoid; *SQ*, squamosal; **S.SCP**, supra-scapula; *sus*, suspensorium; **TI.FI**, tibio-fibula; *tr.pr*, transverse process; **UST**, urostyle; **V.1**, cervical vertebra; **V.9**, sacral vertebra; *VO*, vomer; *I–V*, digits. **B**, the fourth vertebra seen from the front; *a.zyg*, anterior zygopophysis; *cn*, centrum; *lm*, lamina; *n.sp*, neural spine; *tr.pr*, transverse process. (Redrawn after Parker and Haswell.)

whose main function was to support the gills. In the frog larva, or tadpole, there are six pairs of VISCERAL ARCHES, which in the course of development become profoundly modified from the original ancestral condition and are transformed into structures quite different in function. The first pair of these arches goes to form the framework of the upper and lower jaws, while the others either

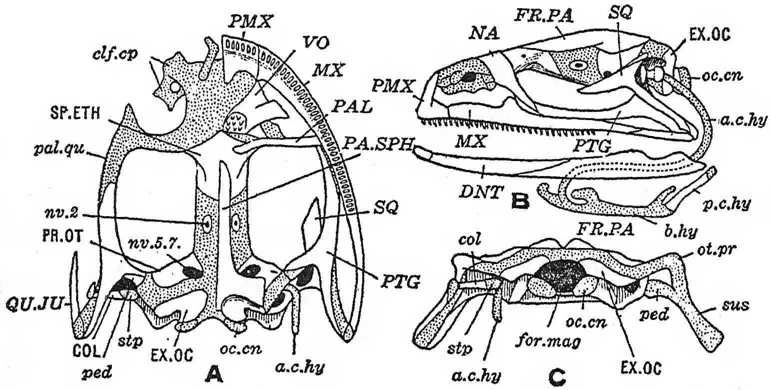


FIG. 208. Skull of *Rana temporaria*. **A**, from beneath with membrane bones removed from the right side (left of figure); **B**, from the left side showing the lower jaw and hyoid; **C**, from behind. Names of cartilage bones in bold; those of membrane bones in italic capitals. Only those parts not already explained in legend of Fig. 207 explained here. *b.hy*, body of hyoid; **COL**, columella; *DNT*, dentary; *for.mag*, foramen magnum; *NA*, nasal; *nv.2*, optic foramen; *nv.5.7*, foramina of the fifth and seventh nerves; *oc.cn*, occipital condyle; *PAL*, palatine; *pal.qu*, palato-quadrate; *PA.SPH*, parasphenoid; *ped*, pedicle; *PTG*, pterygoid; *QU.JU*, quadratojugal; *stp*, stapes. (Redrawn after Parker and Haswell.)

disappear entirely or are reduced to a relatively vestigial condition as HYOID and LARYNGEAL CARTILAGES.

The skull is at first entirely cartilaginous, and is known as the CHONDROCRANIUM. This might be characterized as a tough capsule surrounding the brain. The cartilaginous capsules of the olfactory and auditory organs become fused with the chondrocranium to form a more complex skull. The adult cranium is also reinforced by membrane, or dermal, bones. Meanwhile the original chondrocranium undergoes partial ossification, resulting in the formation or a definite complex of separate bones between which are sutures. In Figures 207 and 208 the bones of the skull are shown in such a way that the reader may readily distinguish the cartilage

bones from the membrane bones, for the cartilage bones are stippled. The cartilage bones are:—SPHENETHMOIDS, EXOCCIPITALS, PROÖTICS, PTERYGOIDS, QUADRATES (still cartilaginous), and PALATINES. The membrane bones are:—NASALS, FRONTOPARIETALS, PREMAXILLARIES, MAXILLARIES, QUADRATOJUGALS, SQUAMOSALS, VOMERS, and PARASPHENOIDS. In the lower jaw there is one pair of cartilage bones, the MENTOMECKELIANS, not shown in the figures; and there are two pairs of membrane bones, the DENTARIES and the ANGULOSPLENIALS.

b. The Appendicular Skeleton (Fig. 207).—The fore and hind leg bones together with the PECTORAL and PELVIC GIRDLES comprise the appendicular skeleton. The PECTORAL GIRDLE consists of: a dorsal flat cartilage, the SUPRASCAPULA; a bone ventral to this, the SCAPULA, in which lies the cup-shaped socket into which fits the rounded head of the humerus; the CLAVICLE, or collar bone, making up the anterior, ventral part of the girdle; beneath the clavicle lies the PROCORACOID cartilage; and the CORACOID bone, forming the posterior, ventral part of the girdle. There is a chain of small bones and cartilages lying between the ventral ends of the pectoral girdle which constitute the STERNUM, or breastbone. To the pectoral girdle are attached the bones of the arms, or forelegs. The bone articulating ball-and-socket fashion with the scapula is the HUMERUS. Next comes the composite RADIO-ULNA, made by the fusion of two separate bones, radius and ulna, that are separate in man and most other vertebrates. Then come the wrist (CARPAL) bones, of which there are six. Finally come the PHALANGES, or finger bones.

The PELVIC GIRDLE consists of a firmly united complex of three elements; the long ILIUM bones, articulating with the transverse processes of the last sacral vertebra; the PUBIS, a cartilaginous element comprising the anterior, ventral part of the girdle; and the ISCHIUM, making up the posterior, ventral portion of the crest of the girdle. The socket, or ACETABULUM, occurs at a meeting place of all three bones. Into this socket fits the head of the FEMUR, or thigh bone. Next to the femur comes a compound bone, the TIBIO-FIBULA, made up by the fusion of the originally separate tibia and fibula. Next to these are the TARSAL, or ankle bones, two of which, CALCANEUM and ASTRAGULUS are much enlarged and the others correspondingly reduced, or absent. The terminal, or distal, bones are the posterior phalanges, or toe bones.

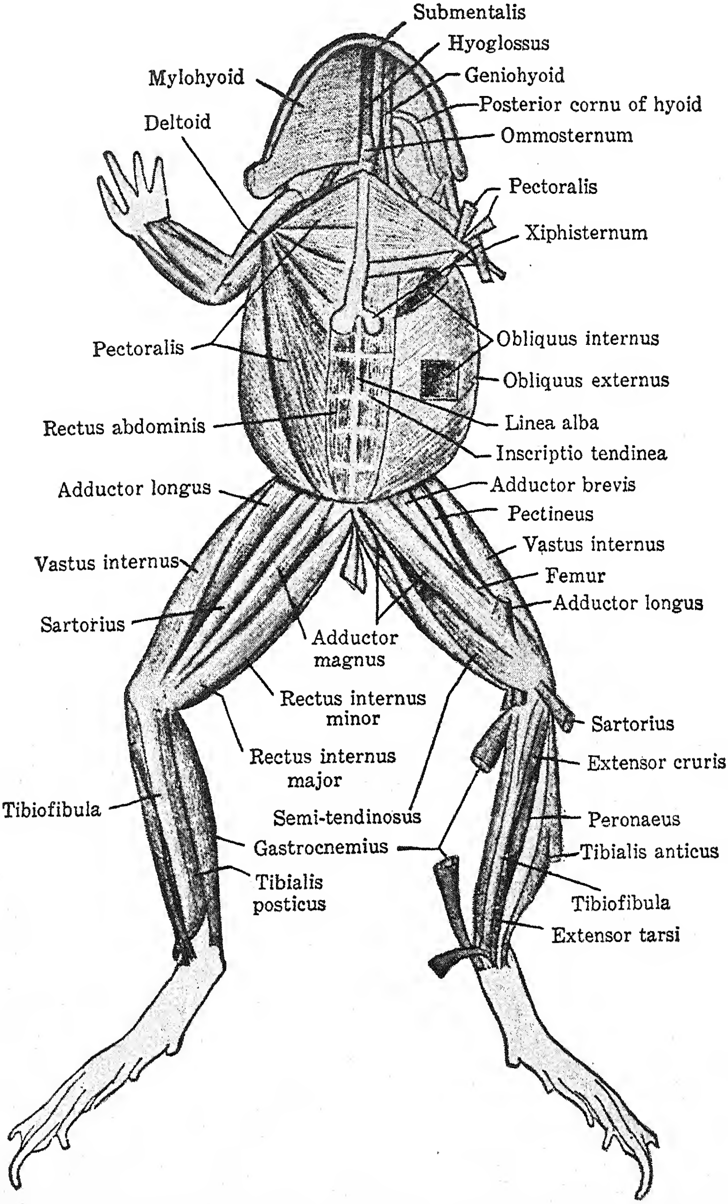


FIG. 209. Muscles of the frog, ventral view. (After Parker and Haswell.)

2. *The Muscular System*

The muscles of the body wall have already been referred to. The remaining voluntary muscular system consists of the muscles of the limbs (Fig. 209). A typical voluntary muscle, such as the GASTROCNEMIUS, has the following parts: the TENDON, a tough cordlike portion attaching the muscle to a bone or to another muscle; the FASCIA, the glistening membrane surrounding the muscle; the BELLY, or fleshy part of the muscle. We call the more fixed attachment point of the muscle the ORIGIN, and the less fixed point the INSERTION. With this introduction the student should be in a position to gain a concrete idea of the muscular complex of the frog by making a laboratory dissection of one or more systems, such as that of the hind leg. One may find in any good laboratory manual directions for this valuable exercise. It seems well in this place to refrain from any attempt to describe in detail the muscular system of the frog.

An extensive system of INVOLUNTARY MUSCLES is found in connection with the movable vital organs, such as the heart, the alimentary tract, the bladder, etc. The histology of muscular tissues is dealt with in a subsequent chapter.

3. *The Circulatory System*

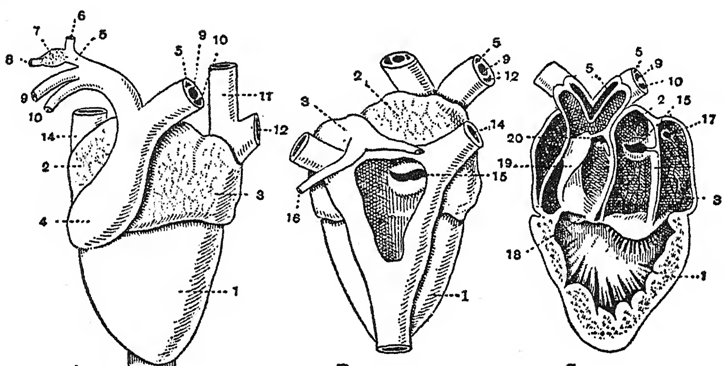
This system consists of the heart, the veins, the arteries, and the capillaries.

a. The Heart.—The heart consists of four main parts: the sinus venosus, the right and left auricles, and the ventricle (Fig. 210). Such a heart is known as three-chambered in contrast with that of birds and mammals, which have four chambers, two auricles and two ventricles. The SINUS VENOSUS is a large, thin walled vessel formed by the union of the three venæ cavæ. It enters the RIGHT AURICLE, which is also thin walled and larger than the left auricle. The right auricle opens into the ventricle through a valve, the auriculo-ventricular valve. The VENTRICLE acts as a forcepump, driving the blood out through the TRUNCUS ARTERIOSUS into the AORTIC ARCHES and thence all over the body. The truncus is provided with a SPIRAL VALVE, sometimes called the longitudinal valve. Between the truncus and the ventricle there are two SEMILUNAR VALVES whose function it is to prevent back flow of the blood when the ventricle expands. The truncus divides into two

main trunks right and left, each of which subdivides into the three aortic arches described later.

b. The Venous System.—This comprises all vessels carrying blood toward the heart (Fig. 211). It may be subdivided into four main sections: SYSTEMIC, HEPATIC PORTAL, RENAL PORTAL, and PULMONARY.

The SYSTEMIC SYSTEM consists of the large single postcaval and the paired precaval veins. Each precaval receives blood from



A B C

FIG. 210. Heart of the frog. A, ventral view. B, dorsal view. C, ventral wall removed. 1, ventricle; 2, right auricle; 3, left auricle; 4, truncus arteriosus; 5, carotid arch; 6, lingual artery; 7, carotid gland; 8, carotid artery; 9, systemic arch; 10, pulmocutaneous arch; 11, innominate vein; 12, subclavian vein; 13, vena cava inferior; 14, vena cava superior; 15, opening of sinus venosus into right auricle; 16, pulmonary vein; 17, aperture of entry of pulmonary vein; 18, semilunar valves; 19, longitudinal valve; 20, point of origin of pulmocutaneous arch. (From Shipley and MacBride, after Howes.)

several large vessels, the external jugular, the internal jugular, and the subclavian veins, the latter in turn receiving blood from the brachial and the musculocutaneous veins. The postcaval receives blood from the paired hepatic veins, from six pairs of renal veins, and from either spermatic or ovarian veins, depending on the sex of the individual.

The HEPATIC PORTAL SECTION consists of a number of veins that, instead of carrying blood directly to the heart, divert it to the liver, where it is chemically altered in various ways before it is returned to the systemic section through the hepatic veins that connect directly with the postcaval.

The RENAL PORTAL SECTION comprises several large veins that

divert a considerable part of the blood returning from the hind legs and visceral organs through the kidneys, where it is purified of some of its waste products before it escapes from the kidneys through the renal veins. These empty into the postcaval vein,

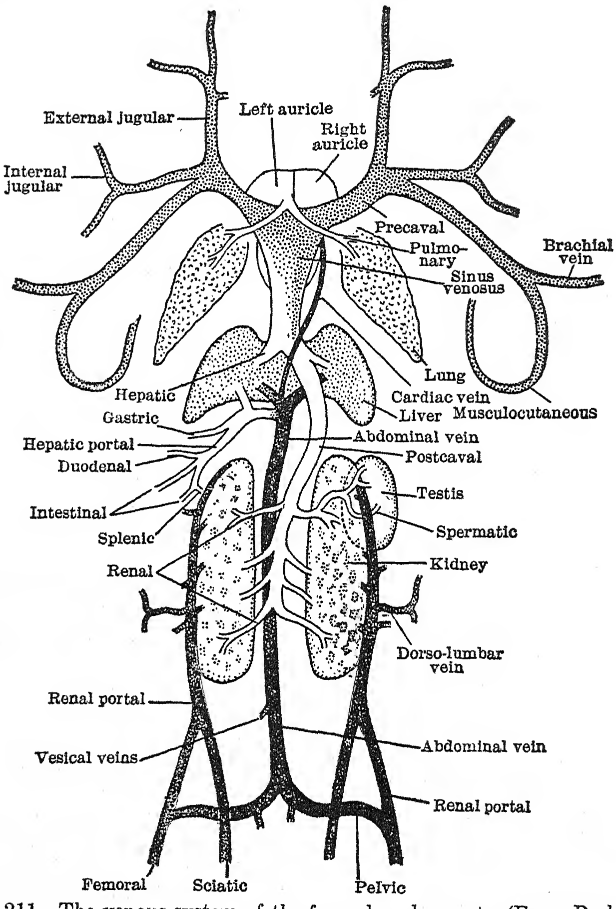


FIG. 211. The venous system of the frog, dorsal aspect. (From Parker and Haswell.)

which also receives blood from the HEPATIC VEINS before it empties into the sinus venosus.

The PULMONARY VEINS are rather small in the frog, carrying blood from the lungs to the heart. Here we have the unusual situation of a vein carrying purified, or oxygenated, blood.

c. The Arterial System.—All vessels carrying blood away from the heart comprise the arterial system (Fig. 212). The three most anterior arterial trunks are the vestiges of three of the ancestral branchial arches. These are the carotid, the pulmocutaneous, and the systemic arches. The CAROTID ARCH divides into internal and external carotids, both carrying blood to the head;

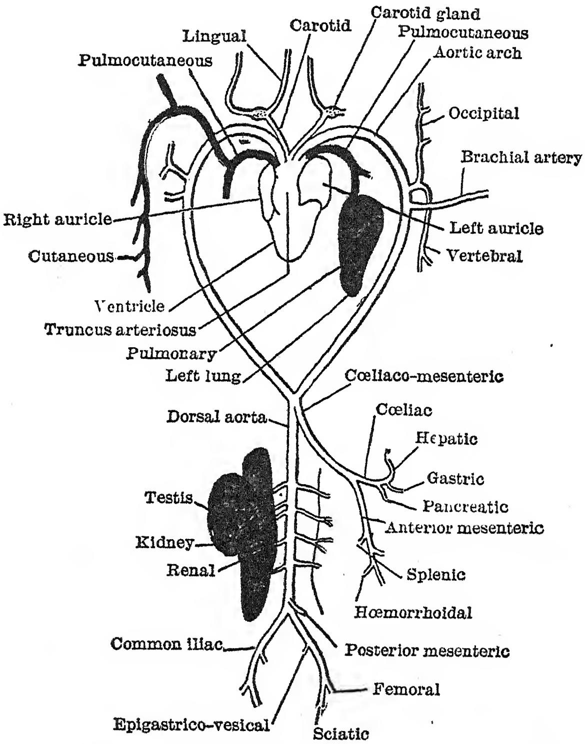


FIG. 212. The arterial system of the frog, ventral view. (From Parker and Haswell.)

the PULMOCUTANEOUS is chiefly respiratory in significance as it carries blood to the lungs and the skin; the SYSTEMIC ARCH supplies purified blood to the viscera and the limbs. The two systemic arches are known as AORTÆ. These unite back of the heart into the single dorsal aorta. Before this union, however, each aortic arch gives rise to a brachial and an occipitovertebral artery that divides into occipital and vertebral. The DORSAL AORTA branches

into the following vessels in the order given: cœliacomesenteric, which soon divides into many branches supplying stomach, pancreas, liver, spleen, etc.; the several pairs of renal, or urogenital, arteries; the posterior mesenteric artery; and finally the aorta bifurcates to form the paired common iliac arteries, the branches of which go mainly to the hind legs.

4. *The Respiratory System*

One commonly thinks that only such organs as lungs or gills are entitled to be designated respiratory organs, but the frog is able to survive for months after its lungs are removed, provided that the surrounding temperature be kept reasonably low. The explanation of this is that the soft, moist SKIN of the frog is an accessory respiratory organ of great importance. That is the reason why a frog can stay under water so long, for it respires through the skin at all times. The LUNGS, however, are definitely differentiated respiratory organs. They consist of a pair of rather simple sacs communicating with the mouth cavity by means of the GLOTTIS, an opening at the base of the tongue, which leads to the LARYNX. The mechanism of inspiration and expiration differs radically from our own. In our own case air is sucked in by enlarging the chest cavity by means of diaphragm and ribs; but in the frog the air is pumped in by muscular contractions of the mouth cavity. When the pressure in the mouth cavity is lowered the air comes back from the lungs to the mouth because of the elasticity of lungs and body wall. The frog has no windpipe, or trachea, a passage with stiff walls, adapted especially to the suction type of inspiration, for it prevents collapse of the intake tube.

5. *The Digestive System*

Little need be said about the general morphology of the digestive system. It is a relatively short food tube, for the frog is carnivorous in the adult state. In Figure 213 one can readily trace the tube from mouth to anus. Note the very short GULLET, or ŒSOPHAGUS; the STOMACH, seen as a spindle-shaped enlargement; the slender SMALL INTESTINE, somewhat coiled; the LARGE INTESTINE, or RECTUM; and the CLOACA into which also open the ureters, the bladder, and the genital ducts. Integral parts of the digestive tract are the digestive glands, LIVER and PANCREAS. These are derived embryonically as diverticula of the digestive tract and

are connected with the latter by means of ducts, the BILE DUCT leading from the liver into the small intestine, and the PANCREATIC DUCT emptying into the small intestine a little closer to the stomach. The whole alimentary tract is slung to the dorsal body wall by sheets of tissue, or MESENTERIES, that serve also as a bridge

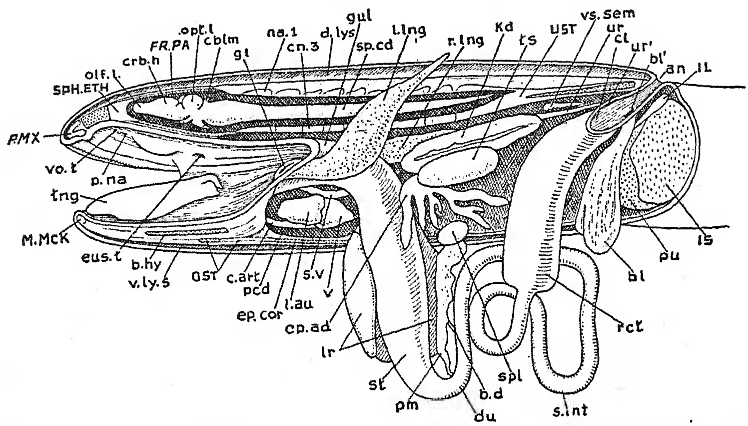


FIG. 213. General internal anatomy of male frog seen from the left side, the viscera somewhat displaced. *an*, anus; *b.d*, bile duct; *b.hy*, body of hyoid; *bl*, bladder; *bl'*, its opening into cloaca; *c.art*, conus arteriosus; *cblm*, cerebellum; *cl*, cloaca; *cn. 3*, centrum of third vertebra; *cp.ad*, corpus adiposum; *crb.h*, cerebral hemisphere; *d.ly.s*, dorsal lymph sinus; *du*, duodenum; *ep.cor*, epicoracoid; *eus.t*, eustachian tube; FR.PA, fronto-parietal; *gl*, glottis; *gul*, gullet; IL, ilium; IS, ischium; *kd*, kidney; *l.au*, left auricle; *l.lng*, left lung; *lr*, liver; M.MCK, mento-meckelian; *na. 1*, neural arch of the first vertebra; *olf.l*, olfactory lobe; *opt.l*, optic lobe; O.ST, omo- and epi-sternum; *pcd*, pericardium; PMX, premaxilla; *pm*, pancreas; *p.na*, posterior naris; *pu*, pubis; *rct*, rectum; *r.lng*, right lung; *s.int*, small intestine; *sp.cd*, spinal cord; SPH.ETH, sphenethmoid; *spl*, spleen; *st*, stomach; *s.v.*, sinus venosus; *tng*, tongue; *ts*, testis; *ur*, ureter; *ur'*, its opening into the cloaca; UST, urostyle; *v*, ventricle; *v.ly.s*, ventral lymph sinus; *vo.t*, vomerine teeth; *vs.sem*, seminal vesicle. (Redrawn after Holmes.)

over which the blood vessels of the viscera may connect with the main arterial and venous trunks.

6. *The Urogenital System*

As in other vertebrates, there is in the frog a sort of amalgamation of the excretory and the reproductive systems. The amount and kind of combination of the two systems differs in the two sexes.

a. The Male Urogenital System (Fig. 214).—Each of the paired oval TESTES is slung from the wall of the body cavity by means of

a mesentary, or MESORCHIUM. Leading from each testis are several small sperm ducts, the VASA EFFERENTIA, that penetrate the kidney. These little ducts are modified nephric tubules that have ceased to play an excretory rôle and are now genital ducts until they unite in the kidney to form a common duct for both urine and spermatic fluid. This common duct, which is both URETER and VAS DEFERENS, empties into the cloaca. A storage sac for spermatozoa, the SEMINAL VESICLE, opens into the ureter.

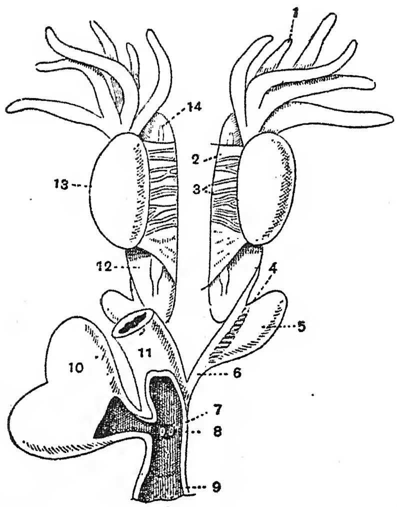


FIG. 214. The urino-genital organs of the male frog, dissected from the front after removal from the body. 1, fat body; 2, fold of peritoneum supporting the testis; 3, efferent ducts of testis; 4, ducts of vesicula seminalis; 5, vesicula seminalis; 6, archinephric duct; 7, cloaca; 8, orifice of ureter; 9, proctodæum; 10, allantoic bladder; 11, rectum; 12, kidney; 13, testis; 14, adrenal body. (From Shipley and MacBride, after Howes.)

b. The Female Urogenital System.—The OVARIES (Fig. 215) are large and conspicuous, especially during the breeding season when they are more massive than the remaining viscera. Each ovary is slung from the dorsal wall of the body cavity, by a mesentery, the MESOVARIUM. The OVIDUCTS are large convoluted tubes, one on each side of the body cavity. The free anterior end of each oviduct is in direct communication with the cœlomic cavity by means of an opening, the OSTIUM, which is ciliated and sweeps the eggs from the body cavity into the oviduct. The main part of the oviduct is glandular and secretes the gelatinous envelope that covers the eggs. The lower part of the oviduct is enlarged into a thin-walled, distensible chamber, the UTERUS, which in turn opens into the cloaca. The KIDNEYS and URETERS are much the same as in the male, but in the female there is no need to use the ureter as a genital duct, for the oviduct serves this function. Attached to both ovaries and testes are conspicuous orange colored FAT BODIES, which though

seemingly parts of the urogenital system, are merely organs of food storage.

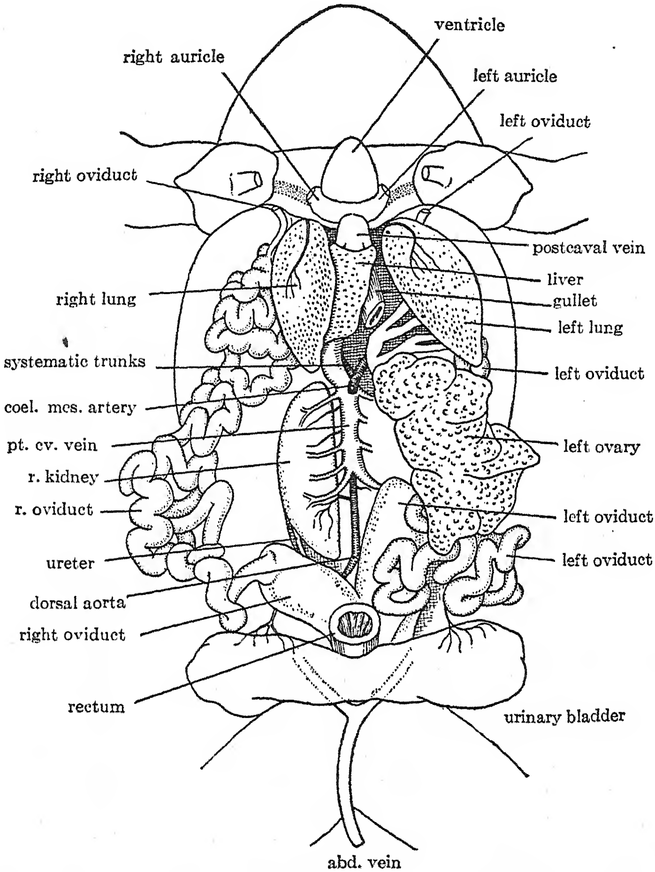


FIG. 215. Organs of a female frog. The alimentary canal has been cut off at the gullet and rectum and most of the liver has been removed. The right ovary and fat body are also removed and the ventricle of the heart turned forward. (Redrawn after Parker and Haswell.)

7. *The Nervous System*

This may be divided into three parts: the central, the peripheral, and the sympathetic nervous systems. The CENTRAL NERVOUS SYSTEM consists of the BRAIN and the SPINAL CORD; the PERIPHERAL NERVOUS SYSTEM consists of the CRANIAL and SPINAL NERVES that run to all parts of the body; and the SYMPATHETIC NERVOUS

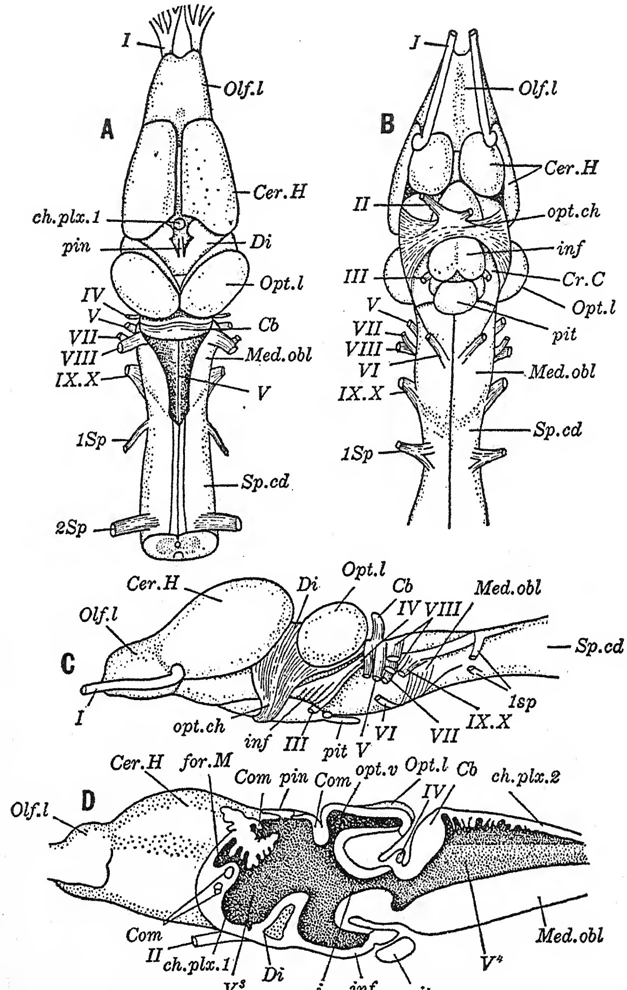


FIG. 216. Brain of the frog. **A,** dorsal side; **B,** ventral side; **C,** left side; **D,** in vertical longitudinal section through the middle. *Cb*, cerebellum; *Cer.H*, cerebral hemispheres; *ch.plx.1*, anterior, and *ch.plx.2*, posterior choroid plexus; *Com*, commissures connecting right and left halves of the brain; *Cr.C*, crura cerebri; *Di*, diencephalon or thalamencephalon; *for.M*, foramen of Monroe; *i*, iter, or aqueduct of Sylvius; *inf*, infundibulum; *Med.obl*, medulla oblongata; *Olf.l*, olfactory lobe; *opt.ch*, optic chiasmus; *Opt.l*, optic lobe; *opt.v*, optic vesicle; *pin*, pineal body; *pit*, pituitary body; *Sp.cd*, spinal cord; V^3, third ventricle; V^4, fourth ventricle; *I–X*, cranial nerves; *1Sp*, *2Sp*, first and second spinal nerves. (Redrawn after Parker and Haswell.)

SYSTEM consists of a group of nerve masses or GANGLIA, together with their connectives, and are associated with the control of the involuntary activities, such as digestion and circulation.

The BRAIN (Fig. 216) is enveloped in a darkly pigmented membrane, the PIA MATER. The chief sections of the brain are the fore-brain, the mid-brain, and the hind-brain. The FORE-BRAIN consists mainly of a pair of elongated OLFACTORY LOBES separated by a longitudinal shallow groove, and a pair of small, poorly developed CEREBRAL HEMISPHERES. The MID-BRAIN is made up chiefly of the THALAMENCEPHALON and the OPTIC LOBES. The HIND-BRAIN comprises the very small CEREBELLUM and the large MEDULLA OBLONGATA.

Ten pairs of CRANIAL NERVES (Fig. 216) come off in serial order and run to various regions as follows:—The first nerves are olfactory, running to the organ of smell; the second pair, optic nerves, run to the retina of the eyes; third, fourth, and sixth nerves are very small and innervate the muscles of the eyeball; the fifth pair of nerves come off from the anterior part of the medulla and are among the largest of the cranial nerves, innervating upper jaws, and other parts of the head; the seventh pair has many branches running to various parts of the head including the lower jaw, lining of mouth, etc.; the eighth, or auditory nerves, innervates the inner ear exclusively; the ninth innervates the mucous membranes of the tongue and the pharynx; the tenth, or vagus, has two branches, one running to the eardrum, the other to the heart, the stomach, lungs, œsophagus, and larynx.

Because of the purely factual character of the material, no summary of this chapter is attempted.

CHAPTER XXXIV

GENERAL PHYSIOLOGY OF THE FROG

ALTHOUGH this chapter deals specifically with the physiology of one animal, the frog, it will also serve as an introduction to physiology in general; for essentially the same functional phenomena as are here to be dealt with appear in man and in most other highly organized animals. No attempt will be made to present in detail the whole physiology of the frog; rather, an effort will be made to make clear the essential features of a few of the most important processes, such as digestion, respiration, circulation, excretion, and some phases of the physiology of the nervous system.

A. PHYSIOLOGY OF DIGESTION

The purpose of digestion is to break down complex food materials, such as proteins, fats, carbohydrates, into simpler compounds capable of being assimilated by the cells of the organism and either elaborated into new protoplasm or used for fuel in the energy traffic of the body. The proteins are the most essential of these three types of food. In addition to carbon, oxygen, and hydrogen, which they possess in common with carbohydrates and fats, they contain also nitrogen, without which life seems to be impossible. In the process of digestion the various kinds of food materials are acted upon by specific ferments, ENZYMES, which hasten the conversion of insoluble substances into soluble ones capable of passing through the membranes of the digestive tract and thus reaching the blood stream.

Let us now trace the food through the alimentary tract, noting the various changes it undergoes at various stages of its course.

Since the frog does not masticate its food, but swallows it whole, there is no mouth digestion such as is to be found in man and other mammals with salivary glands—glands that secrete digestive ferments which take the initiative in breaking down carbohydrate foods.

a. Glands of the Stomach.—The frog's digestion begins in the stomach. There are two kinds of stomach glands: those situated at the CARDIAC end, which are longer and rather deep-set; and

those at the PYLORIC end, which are shorter and less deep. These glands secrete GASTRIC JUICE, a fluid containing about 0.4 per cent hydrochloric acid, a ferment, or enzyme, called PEPSIN, and a number of inorganic salts. Pepsin acts directly upon the proteins, converting them into soluble substances known as PEPTONES. Stomach digestion is a relatively slow process in the frog. It requires fully twenty-four hours completely to digest a small earthworm, and much longer if several worms are eaten at once.

b. The Pancreas.—The partially digested food passes out of the stomach through the PYLORIC VALVE and enters the DUODENUM. While in this part of the intestine a secretion from a large irregular gland, the PANCREAS, is mixed with the food. PANCREATIC JUICE is alkaline, owing to the presence of sodium carbonate (Na_2CO_3). It contains three ferments, or enzymes: STEAPSIN, whose action splits fats into glycerin and fatty acids; AMYLOPSIN, by means of which starch is converted into sugar; and TRYPSIN, which completes the conversion of peptones and undigested proteins into AMINO-ACIDS. Trypsin differs from pepsin in that it acts in an alkaline instead of an acid medium.

c. The Liver.—This is a large gland whose secretion is a greenish fluid, termed BILE. This fluid is mixed with pancreatic juice in the bile duct before it enters the duodenum. Bile is stored in the GALL BLADDER until needed. The glandular cells of the liver, HEPATIC CELLS, are arranged so as to form a branching system of tubular glands communicating with BILE CAPILLARIES; these in turn unite into larger vessels, these into still larger, till the largest branches unite to form the BILE DUCT. The action of the bile is not fully understood. Some of its constituents are believed to be no more than waste products; others almost certainly aid in digestion, having much to do with the conversion of fats into a soapy emulsion that is readily digested by the enzyme, steapsin. Another important function of the liver is that of elaborating and storing GLYCOGEN, a carbohydrate material having the same empirical formula as starch $(C_6H_{10}O_5)_n$, and hence called "animal starch." The quantity of glycogen in the liver varies greatly with the season of the year, being lowest in the spring and highest in the early fall. This seems to indicate that the liver is an important storehouse of reserve food.

d. Absorption of Food in the Intestine.—When the food leaves the stomach and passes into the intestine, it is strongly acid, due

to the hydrochloric acid of the gastric juice. While in the duodenum the acidity is neutralized by the alkaline elements of the bile and the pancreatic juice. Food still undigested is further broken down in the intestines. After digestion is complete the dissolved foods of various kinds are absorbed by the intestinal cells and passed by osmosis into the blood and lymph.

e. Disposal and Use of Food in the Body.—Foods are used to build up tissues and to furnish energy for bodily activities. The proteins are the only foods that can furnish the amino-acids necessary for building proteins in the cell. Fats are, for the most part, stored in cells as droplets. Some fat in adipose tissue is a by-product of the breakdown of carbohydrates and proteins. Fats and carbohydrates function chiefly as fuels. They are combusted by being combined with oxygen and converted mainly into CO_2 and water. Proteins are also constantly being broken down for energy production. There is no sharp distinction between tissue-building and energy-producing foods; for even fats and carbohydrates go to form certain parts of the tissues. After the food materials have been broken down in the process of energy production there are various waste products that must be eliminated through the organs of respiration and excretion.

B. Physiology of Respiration

a. Chief Respiratory Organs.—In the frog the chief respiratory organs are the lungs and the skin, and these share about equally in this important duty.

The lungs are rather simple structures as compared with the lungs of man, and are considerably less efficient. They are thin walled sacs, ovoid in form and capable of great distension. The inner surface is subdivided by means of septa into a number of small compartments, ALVEOLI, which serve to increase the amount of surface exposed to the air. An intricate network of capillaries lies just beneath the surface and affords a ready means of exchange between the air and the blood.

b. Respiratory Movements.—Inhalation is largely a matter of swallowing air into the lungs by means of contractions of the buccal cavity. Air comes into the buccal cavity through the nostrils. These are closed by a sort of valve and the glottis is opened, so that when the buccal cavity is contracted, air is forced into the lungs. Exhalation is due partly to the contraction of the muscles of the

body wall and partly to the elasticity of the lungs. The frog does not have movable ribs nor a diaphragm, as has man, and hence has a totally different breathing mechanism.

c. Changes in the Blood during Respiration.—In the main, it may be said that the blood receives oxygen from the air and gives off CO_2 and water into the lungs. Oxygen is taken up and carried mainly by the red blood corpuscles, whose color is due to the presence of a chemical substance known as HÆMOGLOBIN, which has the property of readily uniting with oxygen to become OXYHÆMOGLOBIN. This substance, in turn, holds its oxygen loosely and readily gives it up when in contact with tissues that need oxygen. It is thus an ideal medium for the transfer of external oxygen to internal tissues. The whole process of respiration includes also the exchange of gases in the lungs and the actual oxidation or combustion of various substances in the protoplasm. The latter is perhaps the fundamental respiratory process; the other steps are merely accessory to respiration proper. Oxidation of foods and protoplasmic materials results in the formation of various by-products, some of which are eliminated through the lungs and some through the skin and kidneys.

d. The Skin as a Respiratory Organ.—Important as are the lungs, they are hardly as important in the frog as is the skin. During hibernation the lungs do not function at all, and the whole burden of respiration is thrown upon the skin. Moreover, it is important to realize that, when for long periods frogs are submerged in the water, the skin acts as a sort of gill, for it can respire even better in water than in air. Even if the nostrils are plugged with wax, a frog can live for days in a moist atmosphere, thus using only the skin in respiration. Experiments have shown that the skin gives off more CO_2 than the lungs. Between its two systems the frog is provided against most respiratory emergencies.

C. Physiology of Circulation

a. General.—The circulatory system is mainly a medium of exchange. It serves as a distributing agent, carrying substances from the outside to internal regions and transporting products elaborated in one tissue to various parts that require the stimulus of such products for their normal functioning. Thus it may be said that the circulatory system is also a coördinating factor of great importance.

The circulatory system consists of many specialized parts, each serving a different function. The main functions may be listed under five heads: pumping, carrying food and oxygen to the tissues, distributing these to the ultimate consumers, or individual cells, carrying waste products to their appropriate points of exit, and distributing hormones throughout the body. These various functions are performed by the heart, the arteries, the capillaries, and the veins. Let us consider these separately.

b. The Functions of the Heart.—The heart (Fig. 210) is essentially an automatic muscular force pump. It arises as a specialized region of the venous system and is therefore essentially a tube. In the heart rhythm the contraction begins in the sinus venosus; then the auricles, ventricle, and conus follow in that order. The heart possesses a system of valves between these sections, preventing the backward flow of blood. In the frog there is not a complete separation, as there is in man, between the systemic and the pulmonary circuits, but the blood from the lungs and that from the veins (pure and impure blood) mingles somewhat in the single ventricle, though the outlets are so placed as to reduce such admixture to a minimum.

So automatic in its action is the frog's heart that it will continue to beat for hours or even days after it has been removed from the body, provided only that it be kept in an appropriate medium. Various experiments have proved that the sinus venosus is the pace setter for the heart rhythm. If the sinus be removed or paralyzed, the other regions of the heart beat more slowly than normal and with a less regular rhythm; while an isolated sinus maintains its normal rate of beat. A heart that has ceased to beat spontaneously may be stimulated into renewed activity by electrical or other means.

c. The Arteries.—The main function of the arteries (Fig. 212) is that of conduits, but they also regulate the flow of the blood through the elasticity and contractility of their muscular walls.

d. The Capillaries.—These are extremely fine, thin walled vessels of such small caliber that blood cells sometimes have to roll up or become elongated in order to force a passage through some of the finer branches. Dissolved food substances diffuse out through the capillaries and pass into the tissue cells. White blood corpuscles (leucocytes) are able to pass bodily through capillary walls, going in or out as the occasion demands.

e. The Veins (Fig. 211).—The veins are merely thin walled non-muscular conduits, leading from the capillaries back to the heart. They also pick up foods and waste products as they pass through various important organs.

f. The Blood.—In the frog the blood is composed of a fluid, the PLASMA, with free cells or corpuscles suspended in it. Three kinds of corpuscles are distinguished: red corpuscles, white corpuscles, and spindle cells. The red corpuscles, ERYTHROCYTES, are elliptical in form, with a well-defined nucleus. Seen edgewise, they are rather flat, with a bulge near the center where lies the nucleus. The cytoplasm is stained with hæmoglobin. The white corpuscles, LEUCOCYTES, are much like tiny amœbæ in form, changing shape and moving about among other cells by means of their pseudopodia. By this mode of locomotion they are able to pass through the capillary membranes with ease, pushing aside the thin endothelial cells as they go through, the latter closing up behind them. The most important function of the leucocytes is the result of their ability to engulf and digest foreign bodies. Thus, invading bacteria that are parasitic on the organism and sometimes cause disease are constantly being destroyed. If the attack of these invaders be too long sustained or be carried on with overwhelming numbers, the leucocytes may not be able to cope with it and the organism may succumb. The presence of invading bacteria at any point sets up an inflammation, and this attracts leucocytes from all sides. Usually the battle between the invaders and the defenders results in favor of the latter. Another function of the leucocytes is that of removing by feeding upon them the inevitable fragments of dead and dying cells that have worn themselves out in the performance of some arduous duties. A third type of cellular blood element consists of spindle cells. These cells are not well understood. They seem to partake of the properties of both red and white corpuscles, being able to transform themselves at times into either of these types.

D. Physiology of Excretion

a. General.—The combustion of the various energy forming foodstuffs and the breaking down of living matter gives rise to various products that are of no value to the organism, but, like ashes and smoke of a furnace, must be gotten rid of in order that the metabolic process may go on unhindered. Carbon dioxide is

one of the most abundant of the by-products, but there are many others that are in solution and cannot be eliminated directly through the lungs or through the skin. These dissolved waste products are removed by a special mechanism or system of mecha-

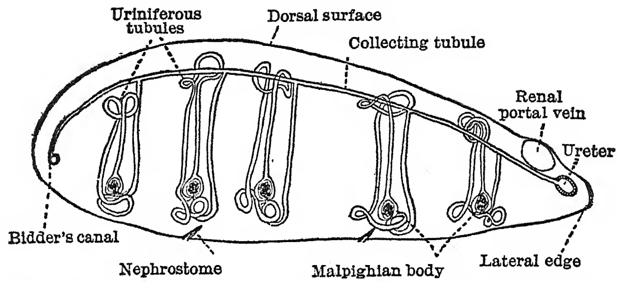


FIG. 217. Diagram of a cross section of the kidney of the frog.

nisms known as the excretory organs. The chief organs of excretion in most animals are the kidneys and the skin. Little is known about skin excretion in the frog, but in the higher forms such as the mammals the sweat glands of the skin perform some share of the excretory duties. The liver also rids the blood of various waste products. We shall, in this account, confine our attention to the function of the kidneys.

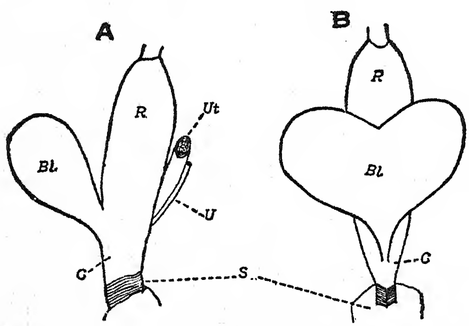


FIG. 218. Diagram of the bladder and rectum of the frog; **A,** from the side; **B,** from below; *Bl,* bladder; *C,* cloaca; *R,* rectum; *S,* sphincter muscle; *U,* ureter; *Ut,* uterus. (Modified from Gaupp.)

b. The Kidneys.—These are two elongated, flattened, dark red organs, lying far back in the body cavity, one on each side of the vertebral column. A kidney consists of a complex system of convoluted URINIFEROUS TUBULES packed in connected tissue (Fig. 217). The distal end of each tubule consists of a bulbous enlargement, the MALPIGHIAN BODY, composed of the inflated end of the tubule, called BOWMAN'S CAPSULE, into which is invaginated a bulbous mass of capillaries, the GLOMERULUS. The liquid wastes pass out

through the walls of the capillaries into the lumen of the Bowman's capsule and flow successively through the uriniferous tubule, the collecting tubule, the ureter, the cloaca, and finally collect in the bladder. The main functions of the kidneys are those of ridding the blood of liquid waste products of protein metabolism and of assisting in the maintenance of the chemical neutrality of the blood.

The kidney secretion, URINE, is a compound of various substances in solution, the chief of which is UREA, $(NH_2)_2CO$, which in the dry state is a white crystalline solid. In addition, the kidney excretes excess salts, principally soluble chlorides of Sodium, Potassium, Calcium, and Magnesium.

c. The Bladder (Fig. 218).—This organ is a storage sac for urine. It is thin walled, bilobed, and opens into the cloaca. It is capable of great distension. The filling of the bladder is effected through the closing of the sphincter muscles of the cloaca, which prevents the escape of the urine and thus causes it to collect in the bladder, whence it may suddenly be expelled by a quick contraction of the body muscles and a corresponding relaxation of the cloacal sphincter muscles.

CHAPTER XXXV

HISTOLOGY OF THE FROG

HISTOLOGY may be defined as that branch of biology treating of the minute (microscopic) structure of tissues. In subdividing an organism into its constituent parts, we find that the largest subdivisions are systems, such as the circulatory system, the muscular system, the reproductive system. A system may consist of several well-defined, specialized parts, each performing some particular function of its own. Such parts are known as organs—typical organs being heart, stomach, liver. Most organs consist of two or more kinds of tissue, so arranged as to work harmoniously together in the performance of a special function. Thus a heart, though composed chiefly of muscular tissue, is made up partly of epithelial tissues, circulatory tissues, nervous tissues, and connective tissues.

A TISSUE may be defined as "a group of cells of similar structure forming a continuous mass or layer." Histology is concerned with the typical arrangements of these tissue cells and with the finer structures of the individual cells.

In the body of the frog, as in those of other animals, we are able to distinguish four main classes of tissues: (1) EPITHELIAL, (2) CONNECTIVE, (3) MUSCULAR, (4) NERVOUS.

Some authorities add a fifth class: BLOOD AND LYMPH TISSUES. These differ in some important respects from other tissues, for they are not groups of cells bound together into membranes or masses, but consist of loose cells floating in the plasma. Whether or not they are to be classified as tissues in the strict sense, they are extremely important ingredients of the organism and will be dealt with in other parts of the text. The four main categories of tissues listed above include a manifold variety of cellular associations and each is to receive separate attention.

A. EPITHELIAL TISSUES

These tissues consist of layers of cells with very little intercellular substance. The commonest function of the epithelial

tissues is that of furnishing coverings for various surfaces, both interior and exterior. Thus, the skin of the frog is an EPITHELIUM, as are also the linings of the body cavities, glands, ducts, and blood vessels. It is customary to classify epithelial cells according to the shapes of the constituent cells. In the outermost skin of the frog (Fig. 219), which is cast off in molting, we have a typical example of flattened or SQUAMOUS EPITHELIUM. The cells are somewhat like flat tiles, slightly bulging at the middle where the nucleus lies and much thinned out at the edges. The cells of the peritoneum are also of this type. In COLUMNAR EPITHELIUM each cell is an elongated column, standing perpendicular to the surface. When these cells are packed tightly side by side they commonly assume the form of hexagonal prisms. Good examples of columnar epithelia are to be seen in the mucous lining of the intestine. Sometimes epithelial tissues are composed of several layers and may contain more than one type of epithelial cells. Such tissues are known as STRATIFIED EPITHELIA. Another type of epithelium very common in the frog is CILIATED EPITHELIUM, a modified form of columnar epithelium in which each cell is provided with cilia at its free end. Such cells are found in the lining of the mouth cavity, the throat, the trachea, the genital and urinary ducts. The synchronous beat of the cilia in one direction creates a current that serves to transport small objects or fluids into or out of a duct, or passage.

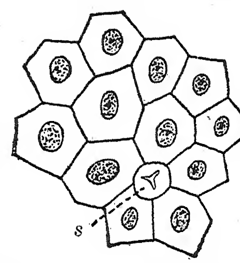


FIG. 219. A portion of the epidermis of *Rana pipiens*. *s*, stoma cell. (From Holmes.)

B. CONNECTIVE TISSUES

This category of tissues includes all sorts of cellular structures that have to do with supporting the body or uniting its various parts solidly into organs. The most striking feature of these tissues is the relatively large amount of intercellular material involved. Some connective tissues are characterized by the presence of one kind of intercellular material, others by that of another. In some, as in bone, the intercellular material becomes hard, owing to the deposit of mineral substances such as calcium carbonate and calcium phosphate. In other tissues, as in cartilage, the intercellular matrix remains relatively soft and elastic. Four principal

kinds of connective tissues are distinguished: *a*, white, fibrous connective tissue; *b*, cartilage; *c*, bone; *d*, adipose tissue.

a. White, Fibrous Connective Tissue (Fig. 220).—Such tissue is very abundant in the frog's body. It is most frequently found in membranes that serve to attach the skin to the deeper layers of the body wall. Microscopically, we note that these tissues are composed of numerous unbranched, wavy fibers, often in bundles, imbedded in a clear, homogeneous matrix. Closely associated with the above tissues are often found YELLOW ELASTIC CONNECTIVE TISSUE FIBERS, which are straight and branched. All three ingredients just mentioned belong to the intercellular part of the tissue. The living cellular ingredients consist of scattered cells, rather small in size and without any particular morphological peculiarities. One finds other types of fibrous connective tissue in the TENDONS and LIGAMENTS and in the muscle sheaths, or FASCIA. ADENOID TISSUE contains also a variety of loose, soft fibrous connective tissue.

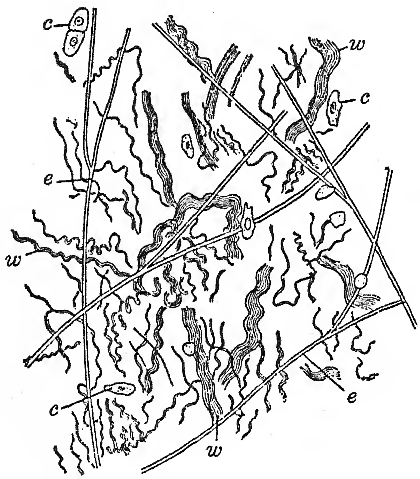


FIG. 220. Fibrous connective tissue from the frog. *c*, connective tissue corpuscles; *e*, elastic fibers; *w*, white fibers. (From Holmes, after Parker and Parker.)

b. Cartilage (Fig. 221).—Cartilaginous tissue is characterized by its massiveness and its density. As a rule it is hyaline or semitransparent. The main bulk of cartilage is the semitransparent intercellular matrix, in which are imbedded at intervals single ovoid cells or groups of such cells, each group probably derived from one divided cell. The cells lie in small rounded cavities within the matrix, known as LACUNÆ. Each cell secretes about itself, layer after layer, a mass of MATRIX material, which in old cartilage forces the individual cells far apart. HYALINE CARTILAGE is found at the ends of the long bones, between the vertebræ, in the skull, in the limb girdles and in various other regions. Most bone originates

through the ossification of cartilage. The skull, for example, is at first a continuous cartilaginous capsule (CHONDROCRANIUM) containing the brain. Various centers of ossification arise and build up the separate bones. CALCIFIED CARTILAGE is a kind of hard cartilage with lime salts in the matrix.

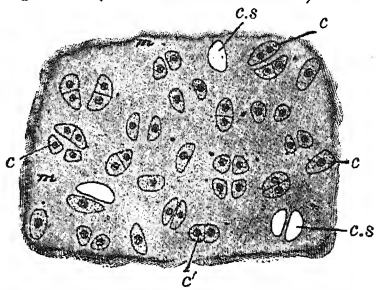


FIG. 221. Cartilage from the head of the femur. c, cells; c', cells in process of division; $c.s$, empty cell space; m, matrix. (After Parker and Parker.)

c. **Bone** (Fig. 222).—Bone commonly has cartilage as a precursor and resembles the latter in general structure. There is the same abundant matrix, here rendered hard through the deposit of lime salts. The bone cells, too, lie in lacunæ. Two types of bone may be distinguished: compact bone and spongy, or cancellous, bone. The former is strong and resistant, the latter relatively weak and loose in texture. A typical bone is the femur of the frog. If a transverse section of it be examined, it is seen to be a hollow tube filled with marrow, a complex tissue composed of adipose, connective, and blood cells. The outer surface of the bone is covered with a membrane (PERIOSTEUM) which consists of cells known as OSTEOBLASTS that are engaged in the manufacture of new bone cells. The main body of the bone is seen to be composed of concentric layers (LAMELLÆ) of hard material in which are imbedded many bone cells, each lying in a separate LACUNA. Fine canals (CANALICULI) connect all adjacent lacunæ one with another, so that all of the living bone cells are in communication with their neighbors.

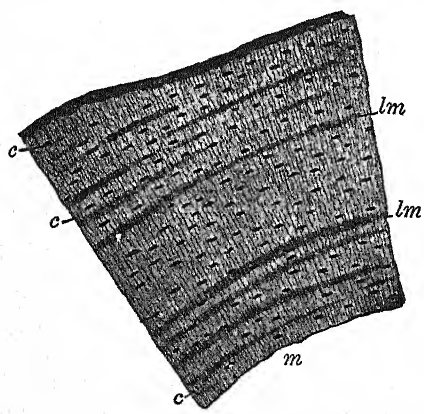


FIG. 222. A part of a cross section of the femur of the frog. c, canaliculi; lm, lamellæ; m, marrow cavity. (From Holmes, after Parker and Parker.)

d. Adipose Tissue.—We may define adipose tissue as storage or packing tissue. The individual cells are gorged with fat and are greatly enlarged. On account of the accumulation of fat in the cytoplasm, the nucleus is crowded to one side of the cell and is flattened against the cell membrane. Sometimes a fat cell seems to be no more than a ball of fat surrounded by a thin film of protoplasm. The fat is secreted by the cytoplasm in the form of small droplets and these droplets enlarge and fuse together so as to form a solid mass.

C. Muscular Tissues

The cells of muscle are called muscle fibers on account of their slender, elongated form. There are two main types of muscle: striated or voluntary, and unstriated or involuntary.

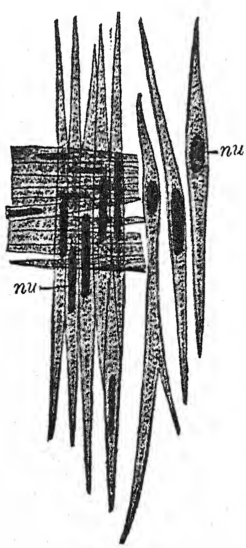


FIG. 223. Unstriated muscle fibers from the intestine of the frog. *nu*, nucleus. (From Holmes, after Howes.)

a. Unstriated Muscle Fibers (Fig. 223).—These are relatively simple in structure. They are spindle-shaped, with the nucleus near the middle. In some organs, notably the bladder, these fibers are very much elongated; while in other organs, notably the walls of the blood vessels, they are relatively short and thick. The longitudinal lines or stripes are due to the presence of slender contractile elements in the cytoplasm, known as FIBRILLÆ. The cell wall of an unstriated muscle fiber is very thin and transparent. These cells are relatively slow and sluggish in their action and are therefore found in organs with slow and regular movements, such as the intestines, the blood vessels, ducts, the bladder, and the ciliary muscles of the iris.

b. Striated Muscle Fibers (Fig. 224).—Fibers of this nature have a more elaborate structure, due to the fact that the cytoplasm is practically all specialized and consists of complex contractile elements. A thin membrane, SARCOLEMMA, surrounds each fiber. In a sense a muscle fiber is a SYNCYTIUM rather than a single cell, for there are numerous nuclei within the

bounds of a single cell membrane. The distinctive feature of these cells is that they are, in addition to being longitudinally striped, transversely striated. The lengthwise striping is due to the presence of numerous closely packed FIBRILLÆ that run from one end of the cell to the other. A small amount of unmodified cytoplasm, SARCOPLASM, separates the fibrillæ from one another. Transverse striation is due to the fact that each fibrilla is divided into a long series of segments, SARCOMERES, separated from each other by thin dark disks of another consistency, known as KRAUSE'S MEMBRANES, which extend not only across each fibrilla but from fibrilla to fibrilla, uniting these into one mass. Several minor elements, the meaning of which is little understood, may also be made out under high powers of the microscope. The mechanism of muscular contractility is still an unsolved problem, though several theories have been proposed to explain it. Striated muscle fibers are found in voluntary muscles and contract quickly to make rapid movement possible.

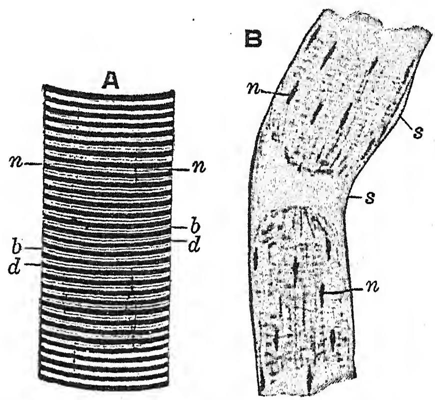


FIG. 224. A, part of a fresh muscle fiber of a frog; B, the same after treatment with distilled water followed by methyl green. *b*, light bands; *d*, dark bands; *n*, nuclei; *s*, sarcolemma showing more clearly where the fiber is broken. (From Holmes, after Parker and Parker.)

c. The Muscle Fibers of the Heart.—Such fibers differ in several respects from those of any other organ. Though they are involuntary, they are striated. Each of the short, thick muscle cells has a single nucleus, and each cell branches so as to join with branches of adjacent muscle cells and thus to form an elaborate network.

D. NERVOUS TISSUES

The cellular elements of the nervous tissues (Fig. 225) consist of nerve cells or NEURONES, which are characterized by the possession of long, slender branches. Two kinds of projections or branches are to be distinguished: those bringing impulses to the nerve cell

body, DENDRITES; and those conducting impulses from the cell body, AXONES.

The body of the neurone (Fig. 225, **D**) is stellate, owing to its branching habit, and has but one nucleus. One neurone may be in contact with another neurone by means of its dendrites or by means of its axone; or it may have both contacts at once, thus acting as an intermediary between two other neurones. The point of contact is known as a SYNAPSE.

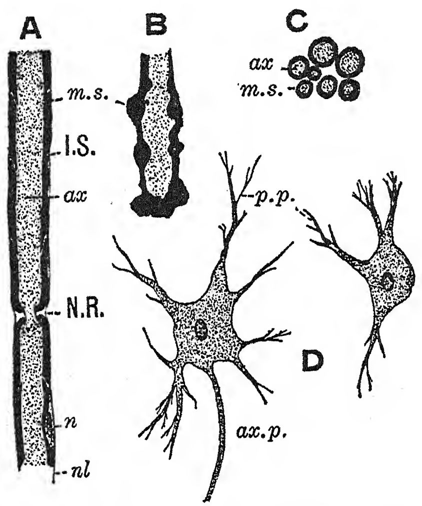


FIG. 225. Nerve cells and fibers of the frog. **A**, fresh nerve fiber. **B**, nerve fiber with the myelin swollen through the absorption of water. **C**, cross section of nerve fibers. **D**, ganglion cells. *ax*, axis cylinder; *ax.p.*, axis cylinder process of ganglion cell; I.S., incisure of Schmidt; *m.s.*, medullary sheath; *n*, nucleus; *nl*, neurilemma; N.R., node of Ranvier; *p.p.*, protoplasmic process of ganglion cell. (From Holmes.)

A single nerve fiber (Fig. 225, **A**) consists of: *a*, a central strand, the AXIS CYLINDER; *b*, an insulating sheath of fatty material, the MEDULLARY SHEATH; *c*, a delicate surface membrane, or NEURILEMMA. The medullary substance is interrupted at intervals, giving rise to constrictions known as NODES of RANVIER. Though the axis cylinder is merely a prolonged outgrowth of a single cell, the medullary sheath is composed of numerous cells, which during growth seek out the extending nerve processes and surround them. These cells are not of nervous origin, but are simply modified mesoderm cells.

When a nerve fiber is cut, the part of the fiber that is separated from the cell degenerates, and the axis cylinder grows out again, following the path of the disintegrating part of the fiber.

Neurones are usually aggregated into masses known as GANGLIA. The brain is a compact mass of ganglia, together with certain other, non-nervous tissues. Other ganglia occur in the spinal cord and in connection with the sympathetic nervous system.

In the brain, as well as in other ganglionic masses, the neurones are connected up in various ways so as to form conduction paths.

Since this chapter is simply a catalog of factual data, no summary seems necessary.

CHAPTER XXXVI

THE DEVELOPMENT OF THE FROG

ONE of the marvels of nature is the development of a complex organism out of a single cell, an egg. We are even more in the dark as to the underlying cause of individual development (ONTOGENY) than we are about racial development (PHYLOGENY or EVOLUTION); yet we may witness, either with the unaided eye or with the enlarging eye of the microscope, every event in the developmental history of an individual. With the help of the compound microscope we can watch the process of cell division and multiplication; we can catch the changes that lead to differentiation of tissues and division of labor among them; we can observe the beginnings of organs and of systems and follow the various steps in their development up to the definitive condition. We can even follow out the smallest details in the gradual making of an eye out of a collection of diverse tissues. We can see the first heart beat, the first appearance of gills, the origin of blood, the formation of the mouth. In fact, we can see the whole moving picture of development; but we do not yet know what makes it develop. Even to the expert embryologist the development of any organism is a sort of miracle, for he knows not the motive power that drives the machine.

We have some knowledge of the mechanisms of development, but the main problem is still unsolved.

A. Theories of Development

Two opposed theories, or types of theory, have been held for many years and by many thinkers: PREFORMATION THEORIES and EPIGENESIS THEORIES.

a. Preformation Theories.—Some of the older writers evaded the issue of explaining the origin of an individual from the egg by predicating that the adult organism is already preformed in the egg or in the spermatozoön. The miniature organism was supposed to be present in an extremely condensed form within the confines of one of the germ cells, needing only to take up water

and food in order to expand or unfold itself into the complete organism. This crude form of the preformation doctrine has given way in recent times to the much more refined conception that all of the characters of the adult are represented by appropriate determiners or genes, which lie in the germ cells and either singly or in groups take part in the realization of the specific characters of the mature organism.

b. Epigenesis Theories.—Other early writers held a view directly opposite to that of preformation; namely, that the germ cell is structureless and homogeneous at the beginning of development and that it acquires organization and complexity largely through the molding influence of the environment and that of one part upon another. Views essentially epigenetic are held today by prominent biologists, but few would accept this theory in its extreme form.

Modern biologists, as a rule, are inclined to strike some sort of compromise between these opposed theories and to hold that much of the type of organization of an individual is predetermined in the fertilized germ cell, but that the environment exercises a profound influence in shaping the course of ontogeny.

B. Development of the Frog

Amphibian embryology, and that of the frog in particular, occupies a very central place in the system of comparative embryology. It will therefore well serve the purpose of illustrating the important steps in ontogeny (the origin of a new individual) and the principles that underlie the science of embryology in general. No better type could well be selected for such a purpose.

1. *The Germ Cells of the Frog*

The frog's EGG is a comparatively large cell, about the size of a buckshot. The upper hemisphere of the egg is black, owing to the presence of many pigment granules. The dark color is believed to be an adaptation for absorbing and retaining heat; for the eggs are laid in early spring when the ponds and streams are very cold, and the egg needs to absorb all of the sun's heat that it can. The egg is surrounded by three layers of transparent JELLY (Fig. 226): a thin layer lying tightly against the cell membrane, a thick middle layer of somewhat fluid consistency, and a thick outer layer some-

what less fluid. The jelly is believed to have a protective function, warding off attacks of bacteria; and it also helps to retain heat, for it has the property of letting in heat rays from the sun more readily than it lets them out. The upper, pigmented part of the egg marks the hemisphere characterized by the presence of the ANIMAL POLE, that region of the protoplasm which is most active and near which lies the nucleus, or GERMINAL VESICLE; the unpigmented hemisphere is the site of the VEGETAL POLE, or yolk pole, the least active region of the egg. The whole egg is surrounded by a delicate cell wall, or VITELLINE MEMBRANE. The arrangement of the pigment and the position of the nucleus are somewhat eccentric and on this account furnish useful landmarks for determining the bilateral symmetry of the undivided egg.

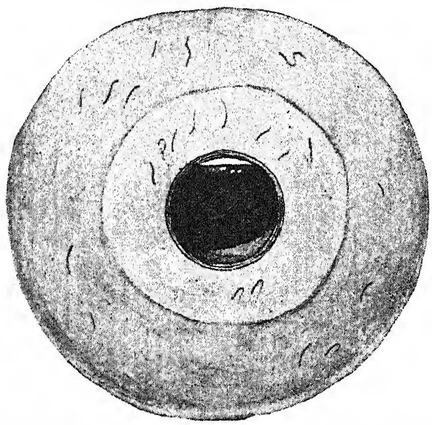


FIG. 226. Egg in jelly. (From Holmes, after Schultze.)

The SPERMATOZOÖN of the frog (Fig. 227) is also a single cell, highly specialized for the one function of fertilizing the egg. It is composed of a spindle-shaped head, a short middle piece, and a long slender tail. The head contains the nucleus which consists largely of a condensed mass of chromatin.

2. *Maturation of the Germ Cells*

Before maturation each male and female cell contains a double set of chromosomes. They occur in pairs, one of each pair having been derived from each parent of the previous generation.

a. The Origin of the Spermatozoön.—We shall describe the origin of the spermatozoön first as it is a little simpler than that of the mature egg. The chromosomes pair off, uniting two and two according to kinds, for only homologous, or equivalent, chromosomes pair. Then a mitotic spindle forms and the paired chromosomes line up in the equatorial plate of the spindle. After

a pause, one chromosome of each pair begins to travel toward each pole of the spindle. Soon two groups of chromosomes are formed, one at one pole and one at the other. The result is that each cell that arises from this division has but a single set of chromosomes, consisting of one of each kind, and therefore has only one half the number of chromosomes that were present in the original sperm cell, or SPERMATOCYTE. This division is known as the REDUCTION DIVISION and the pairing of chromosomes that paved the way for reduction is known as SYNAPSIS. A second maturation division quickly follows, but it is just like any ordinary mitotic division in that each chromosome is longitudinally split into two half chromosomes and no reduction in the number of chromosomes is involved. Thus, as the result of two cell divisions, four SPERMATIDS, each with the HAPLOID (reduced to one half) number of chromosomes, are produced. Each spermatid gradually develops into a mature SPERMATOZOAN.

FIG. 227. Spermatozoön of *Rana esculenta.* (From Holmes, after La Valette St. George.)

b. The Origin of the Egg.—The original egg, oögonium, undergoes a long, slow period of growth at the end of which it is termed an OÖCYTE of the first order. During the growth period chromosome synapsis takes place. The two maturation divisions take place, as in the origin of the spermatozoön, except that the divisions are very unequal with respect to the cytoplasm and yolk, one large cell nearly equal in size to the oöcyte and one small cell (POLAR BODY) being produced at each division. Sometimes the first polar body divides to form two small abortive eggs; and these, together with the second polar body, represent three of the four cells resulting from the maturation divisions. The fourth cell is the matured egg (OÖTID) with the haploid number of chromosomes. The polar bodies (abortive oötids) and the functional egg are alike in nuclear content, but extremely different in cytoplasmic content, for practically all of the cytoplasm that might be expected to be shared by four cells has been appropriated by one. The two kinds of maturated germ cells—spermatozoa and eggs—are known as GAMETES, a term which implies that they are cells that mate.

3. *Fertilization*

The union of two gametes—an egg and a spermatozoön—is the first event of fertilization. This union produces the fertilized egg, or ZYGOTE. The spermatozoön swims to the egg and enters it by penetrating the vitelline membrane. The entrance of one spermatozoön into an egg so alters the chemical character of the latter that no additional spermatozoa can enter. In the frog, only the head of the spermatozoön enters the egg, the tail being discarded. The head of the sperm soon rounds up into a spherical nucleus, known as the MALE PRONUCLEUS. At first this is much smaller than the nucleus of the egg, but it soon increases in size at the expense of the egg cytoplasm until male and FEMALE PRONUCLEI are equal or nearly so. Finally, the two pronuclei, male and female fuse to make the FUSION NUCLEUS and the act of fertilization has been accomplished.

4. *Cleavage*

Development begins with a series of mitotic cell divisions of the zygote or fertilized egg, which occur without any intervening growth. In spite of the rather large mass of yolk present, the cleavage furrows cut through the entire egg; thus cleavage here is total or HOLOBLASTIC. The first and second cleavages (Fig. 228, A, B) are from pole to pole (MERIDIONAL), giving rise to four equal BLASTOMERES. The third cleavage (Fig. 228, C) is slightly above the equator and parallel with the latter, and is said to be EQUATORIAL. This cleavage gives rise to four pigmented and slightly smaller cells of the animal pole (MICROMERES) and four unpigmented and somewhat larger cells at the vegetal pole (MACROMERES). The micromeres, having been derived from the more active region of the egg protoplasm, divide more rapidly than the macromeres, or yolk cells; and hence the cells at the animal pole become considerably smaller and more numerous than those at the vegetal pole (Fig. 228, D). As the cells continue to divide, they form a hollow sphere, the BLASTULA (Fig. 228, E, F), with a fluid-filled cavity known as the BLASTOCŒL, or CLEAVAGE CAVITY. The typical blastula stage in developing organisms is a one-layered stage, with all the cells exposed on the surface. In the frog, however, the large size of the cell and the accumulation of yolk have the effect of causing more or less crowding of some of the cells

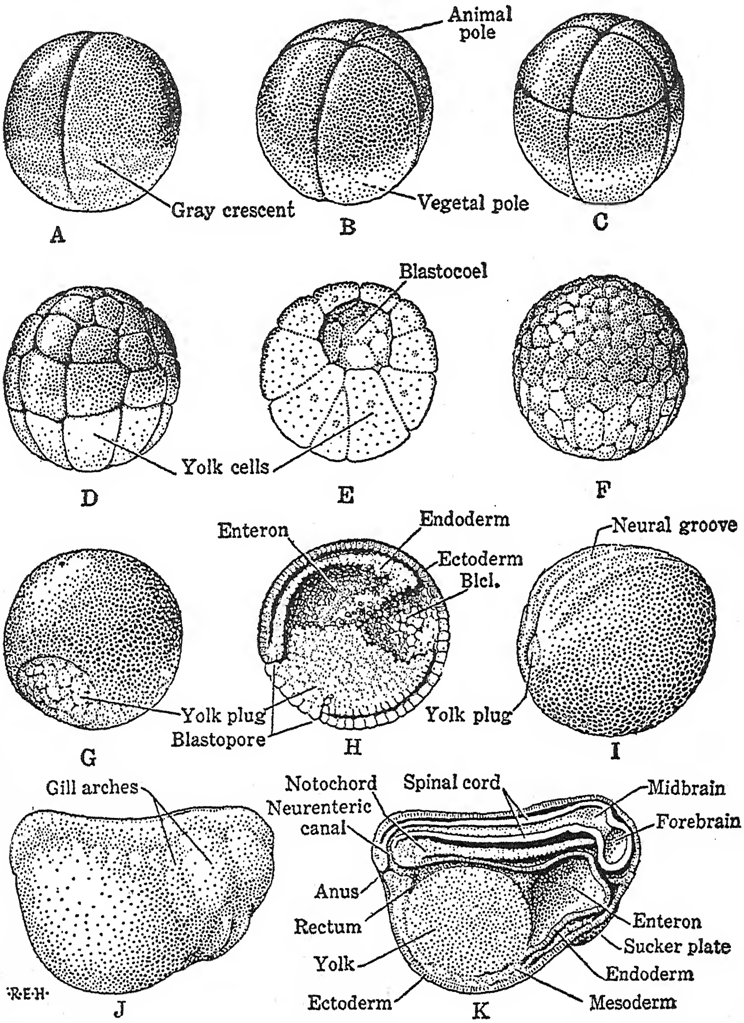


FIG. 228. Early embryonic development of the frog. A, B, C, eggs at two-, four-, and eight-cell stages; D, early blastula; E, section of D; F, late blastula; G, early gastrula: showing ectoderm spreading over endoderm which is all covered but the yolk plug; H, section of G, showing germ layers, etc. (Blcl, blastocœl); I, late gastrula, showing formation of neural groove and folds; J, older embryo with closed neural groove; K, section of J. (From Woodruff.)

from the surface, giving the blastula the appearance of being several cell layers thick in some regions. Since, however, there is no difference between the superficial and the deeper cells, it may be claimed that this blastula is essentially one-layered.

5. *Gastrulation*

Typically, gastrulation consists of the folding in of the larger cells of the vegetal region to form an inner layer of cells called the ARCHENTERON, or primitive intestine. In the frog, the vegetal pole cells, the prospective ENDODERM, are so massive that a simple infolding would be very difficult. The difficulty is partly evaded by having the inpushing (INVAGINATION) of the endoderm take place at the thinnest part of the endoderm where ectoderm and endoderm meet. The archenteron is produced by a flat infolding just below the edge of the pigmented area, leaving a crescentic crease on the surface, which is the BLASTOPORE. Gastrulation is not considered complete until all of the endoderm cells are surrounded by ectoderm; so it becomes necessary for the more actively growing ectoderm cells (Fig. 228, G) to lend their aid. These fold over the exposed endoderm cells, like a cap being pulled over a head, until only a small opening, the true blastopore, is left (Fig. 228, I). The archenteron, at first quite flat, soon expands greatly and fills most of the cleavage cavity. Thus the finished gastrula, whose equivalent is found in nearly all Metazoa, is typically a two-layered stage with a layer of ectoderm outside and a layer of endoderm inside. Some authors use the term ENTERON for archenteron (see Fig. 228, E and K).

6. *Formation of Mesoderm*

Mesoderm formation is accomplished by the ingrowth of a sheet of cells around the margin of the blastopore, where ectoderm and endoderm meet. This zonelike layer soon splits into two sheets, an outer or SOMATIC LAYER and an inner or SPLANCHNIC LAYER, with the secondary body cavity, CŒLOM, between. The median dorsal portion of the archenteron becomes separated off to form the NOTOCHORD, while the at first continuous plates of mesoderm to right and left of the notochord become distinctly segmented into blocks, the MESOBLASTIC SOMITES, that give rise to muscles, etc. The ventral cœlomic mesoderm does not become segmented.

7. *Formation of the Nervous System*

Development of the nervous system is decidedly precocious; for even in a late gastrula stage the MEDULLARY PLATE, a flattened sheet of ectoderm on the dorsal side, is clearly defined. At a time when the blastopore is nearly closed, the dorsal parts of the embryo have shaped themselves into a broad neural groove, flanked on both sides by a pair of MEDULLARY FOLDS (Fig. 228, I), which arch over the groove and meet in the median dorsal line. They fuse together first in the region of the future neck, and from there fusion proceeds both forward and backward until the neural groove is converted into a NEURAL TUBE. The anterior part of the neural tube soon becomes constricted so as to form the three primary brain vesicles, the primordia of the FORE-, MID-, and HIND-BRAINS. During these changes the embryo has been elongating, and before hatching reaches a length nearly three times as great as its breadth.

8. *Larval Period*

At the time of hatching the larva is somewhat fish-like in appearance, with a vertically flattened tail (Fig. 229, **1**, **2**). The mouth is ventral in position and is surrounded by a chitinous rim or scraper, a purely larval feeding organ used for scraping nutritive matter from the surfaces of aquatic plants. Two pairs of branching EXTERNAL GILLS (Fig. 229, **4**), true larval organs, grow out from the sides of the head and act as the first of a series of respiratory organs. Somewhat later a fold of skin (Fig. 229, **5**) appears in front of the gills and grows backward over the main part of the trunk, inclosing the gill region. This skin fold is known as the OPERCULUM. It has on the left side a single opening, the SPIRACLE (Fig. 229, **6**), through which water may be passed from the gill slits to the outside. While the operculum has been growing backward, the external gills have been resorbed, and INTERNAL GILLS, much like those of adult fishes, take their place and constitute the second respiratory system of the developing frog. The frog at this stage has many anatomical features decidedly fish-like in character. Up till now no paired appendages have appeared, but this deficiency is soon made good. The hind legs are the first to develop (Fig. 229, **7–12**), closely followed by the forelegs, which for some time grow underneath the operculum and cannot be seen from the outside. The tadpole at this stage is a strange looking object—

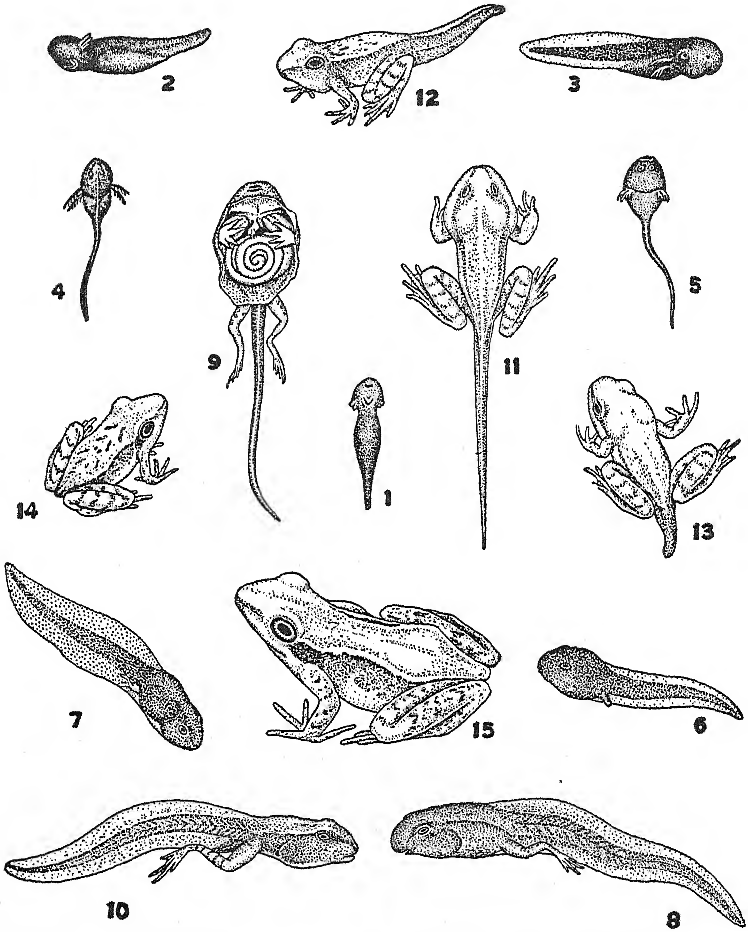


FIG. 229. Larval development of the frog and Metamorphosis. **1,** tadpole just hatched, dorsal aspect; **2, 3,** older tadpoles, side view; **4, 5,** later stages, dorsal views showing external gills and development of operculum; **6,** older tadpole, left side, showing single opening of operculum; **7,** older stage, right side, showing hind leg and anus; **8,** and **10,** lateral view of two later stages showing development of hind legs; **9,** dissection of tadpole to show internal gills, spiral intestine, and anterior legs developed within operculum; **11,** advanced tadpole just before metamorphosis; **12, 13, 14,** stages in metamorphosis, showing gradual resorption of tail; **15,** juvenile frog after metamorphosis. (Redrawn after Leuckart-Nitsche wall chart.)

neither fish nor frog; it is high time for something radical to happen.

9. *Metamorphosis*

The period of metamorphosis (Fig. 229, **12–15**) is really part of the larval period and cannot be marked off sharply from the latter. One phase blends gradually into the other. Toward the close of the larval period the tail begins to be resorbed and the materials derived from its dissolution are stored up in the liver; the long spirally coiled intestine, a typical vegetarian organ, shortens up into the relatively short intestine appropriate for a carnivorous animal; the gills are resorbed and lungs appear and grow rapidly in size. At this time the polliwog comes to the surface to breathe air.

At the end of the period of metamorphosis the animal is no longer a larva, but a juvenile frog. Some species of frog go through their whole development up to the juvenile condition in the course of a few weeks; others require several months; while the northern bullfrog (*Rana catesbiana*) sometimes takes three or four years—even longer larval periods have been reported—to reach the period of metamorphosis; and occasionally specimens remain larval for years, steadily increasing in size until as large as some adults, but remaining polliwogs in every respect except that they become sexually mature. This interesting phenomenon, involving failure to metamorphose and sexual maturity in larvæ, is called NEOTENY and is discussed further in Chapter XLIII.

10. *The Period of Adolescence*

This is a long period, covering the time after the completion of metamorphosis up to sexual maturity. The chief changes involve alterations in the relative proportions of the parts, the head being at first relatively large and the legs relatively small. The young skeleton, largely cartilaginous at first, gradually ossifies. The most significant changes are those that are last to be initiated; namely, those that have to do with the onset of sexual maturity. Shortly before the beginning of the first breeding season, the cells of the ovaries and those of the testes begin to multiply and then to grow rapidly in size; the ducts of these gonads differentiate, and the processes of oögenesis and of spermatogenesis begin—processes that culminate in maturation, the point where we began our description of the frog's life cycle.

SUMMARY

1. The developmental history of the frog illustrates not only the main events of frog development, but those of vertebrates in general and to a certain extent those of invertebrates.

2. The main theories as to why a definite type of animal comes from a particular kind of egg are: *a*, Preformation Theory, which holds that in some way the organization of the animal is preformed in the egg; and *b*, Epigenesis Theory, according to which the organization of the animal is the result of interactions between the substance of the eggs with one another, and with the environment.

3. Biologists today believe that the extent to which organization is preformed in the egg varies with different groups, and that all characters are the expression of internal (genetic) factors interacting among themselves and with factors of the environment.

4. The egg of the frog is fairly large, with yolk accumulated at the vegetal pole.

5. When full grown, the egg undergoes maturation consisting of two nuclear divisions (meiosis) one of which results in the segregation of one of each kind of chromosomes into separate cells (gametes), each with half the somatic number of chromosomes—the haploid number.

6. Sperm cells undergo meiosis, and mature spermatozoa also have the reduced (haploid) number of chromosomes.

7. Fertilization of the egg by the sperm restores the diploid number of chromosomes, the fertilized egg being a zygote.

8. Cleavage takes place through mitosis, the resulting cells being called blastomeres.

9. A hollow blastula is the result of many cleavage divisions.

10. Embolic gastrulation of a modified sort gives rise to a gastrula stage.

11. A long larval period is followed by a period of metamorphosis of the "polywog" into the young frog.

12. The period of adolescence is terminated by the onset of sexual maturity and the maturation of the germ cells, bringing us back to the point in the cycle from which we started.

PART V

BIOLOGICAL MECHANISMS IN GENERAL AND MECHANISMS OF INDIVIDUAL MAINTENANCE AND ADJUSTMENT

CHAPTER XXXVII

BIOLOGICAL MECHANISMS IN GENERAL

According to the mechanistic view of life, a view well nigh universal in professional biological circles, an organism is a kind of machine. By a machine we mean a complex unit made up of many interoperating and coöperating parts, a unit that goes, and performs useful work. Parts of a machine may be appropriately called mechanisms.

A. Living and Lifeless Mechanisms Compared

A living machine resembles a lifeless machine in some important ways, but it differs in equally important ways. For convenience, let us compare a horse, a type of living machine, with an automobile, a type of lifeless machine.

Both the horse and the automobile are complex in structure and are made up of numerous parts that are connected up in definite ways with one another. In both of them every part bears a definite relation to every other part. In both of them the great majority of parts are essential to the functioning of the machine as a whole, but some parts are less essential than others. For example, the horse will go almost as well without a tail or minus an ear, while a motor car will perform as a vehicle as well without bumpers or fenders as with them. For the best functioning under all sorts of conditions, however, both machines need practically all of their parts.

Another resemblance between the horse and the automobile is seen in the fact that the motive power for running must be furnished by materials outside the machine. The automobile must have gasoline put into its tank and must take in air through its carburetor, while the horse must eat hay, oats, or other energy producing materials, must drink water, and breathe air. The chief difference in the fueling of the two machines is that in the case of the car the fuel must be furnished in a highly refined form ready for immediate combustion, while in the case of the horse the fuel taken in is in a very crude state, requiring an elaborate process of

refinement before it is in condition to be used for power production. If the automobile had its own refinery it would be more like a horse.

Once more, the horse and the car have certain parts that are mainly for protection against the dangers of the environment. The car has a hood over the engine, waterproof lacquer over exposed parts, bumpers, springs to prevent jars, cooling and lubricating systems to prevent injury to moving parts, stop signals, horn, lights, and other mechanisms that help to prevent injury or destruction of the machine. Correspondingly, the horse has its most important working parts inside the body, well protected by the body wall and the ribs. It has a waterproof skin covered by a coating of hair to protect the surface, highly perfected temperature regulating mechanisms corresponding to a cooling system, hoofs and teeth to fend off dangerous enemies, and a host of other adaptations for maintenance and protection.

Again, both the horse and the car have centralized motivating parts. The battery and the timer, with their various accessories and connections, in some important ways correspond to the central nervous system of the horse and its connections. By means of this centralized control both horse and motor car exhibit coördination in the operation of all moving parts. In the car centralized control enables all parts to move in harmony, and changes in the speed of one part are accompanied by appropriate changes in all other parts. This is also true for the horse, for there are many synchronized functions, such as rate of respiration, rate of heart beat and circulation, and changes in body temperature, that are very closely correlated.

While there are many correspondences between the horse and the automobile, there are also many differences. You will immediately think of the fact that the horse needs no driver, but can control its own activities. It can get information about its environment and govern its movements accordingly. In contrast with this, the automobile cannot control its course without a human driver; it cannot get its own fuel or other necessities for operation.

Again, the automobile gradually wears out and needs repairs, while the horse repairs its worn parts as fast as they are in need of repair. Then the horse has the capacity of reproducing more horses like itself, a capacity unfortunately totally lacking in the automobile. The horse is able to modify itself in accord with

changes in the environment, as when it grows a heavier coat of hair in cold weather, or when it increases its speed by training. Finally, the horse possesses intelligence, something totally lacking in any lifeless machine. This is hardly the place to discuss the nature and manifestations of intelligence, but we must not fail to realize that it is in this respect that we must draw the sharpest line between the living and the nonliving.

On the whole then it would seem that the differences between the living and the lifeless machine are more impressive than are the resemblances. Even if we go so far as to admit that the characteristics of the living machine that resemble those of the lifeless machine are subject to mechanistic interpretation, does this admission necessarily include those characteristics that are found only in the living? Are we in a position to assume that, because many of the activities of the organism are explained in physicochemical terms, all of the other activities may also be similarly explained? Are all vital activities expressions of mechanisms at work?

B. A Conception of Organic Mechanisms

Our answer to the above questions must depend upon our definition of mechanism. If we define a mechanism as a complex unit all the activities of which are explainable in terms of the known laws of matter and of energy as worked out for lifeless objects, it is obvious that living organisms will fall outside the scope of this definition. If, on the other hand, we define a mechanism as any complex unit in which any sort of transformations of energy and of matter are taking place, we make room for organisms in our definition. In so doing we remain in the realm of material things.

It seems obvious that the arrangement and configuration of chemical substances in life units differ from those in nonliving units, but this does not mean that anything immaterial is introduced at the life level. What it does mean is that when we pass from the lifeless level to the living level of material units there emerges as a consequence of the new order a whole set of entirely new properties that are not in a strict sense inherent in the ingredients of which the life unit is composed. These higher expressions of energy are the product of the organization and configuration of all the component parts. They are what we term vital properties; they are essentially properties of the organism as a whole and depend upon the interaction of all the parts, for if the interrelations

and interactions of parts become seriously deranged the vital properties are lost.

This view does not involve a denial of the mechanistic interpretation of life: it merely extends the definition of mechanism in a legitimate way so as to include a new level of mechanisms. It involves no concession to vitalism, for it introduces no immaterial or mystical forces presiding over the organism. The energies and the materials involved at the life level of units are to be thought of as *natural* materials and *natural* energies.

If then we realize that the most strikingly biological characteristics of organisms emerge only at the organic level of material units, we shall not expect to understand these characteristics solely in terms of the properties of nonliving units. It is our belief that the higher types of biological phenomena can be interpreted only in terms of biological facts and factors. The sooner this comes to be recognized, the sooner will real progress be made in the direction of a distinctive science of biology.

When we intimate that many of the higher vital phenomena are susceptible of analysis only in biological terms, we do not mean to imply that none of the processes going on in organisms are of the simpler sort that are explicable in purely physicochemical terms. The organism must be looked upon as living in a physicochemical environment and hence carrying on a traffic with this environment. It is to be expected that the organism will make use of all chemical or physical means that are useful in the maintenance of its relations with the environment. The fact is that a great many processes in organisms have been shown to be purely physicochemical; that many other processes have physicochemical aspects and accompaniments, though not fully understood in physicochemical terms; but that there are still many biological phenomena that are as yet unintelligible in terms of the physics and chemistry of the nonliving world. It would be rash to say that these phenomena never will yield to physicochemical analysis, but the outlook at the present time is not too hopeful.

In spite of the situation just discussed, it is reasonable to think of organisms and their various integral parts as mechanisms, using the term in the broad sense in which we have defined it. In this definition we shall include all structures and activities that are regular and play a definite and useful part in the life of the organism.

It will be helpful in presenting the facts about biological mechanisms to classify them. The two primary objectives of life, if we may use the word "objective" without implying any idea of purpose, are *a,* those of *individual or self maintenance and adjustment* and *b,* those of *racial maintenance and adjustment.* There is a sort of antagonism between these two objectives. The mechanisms favoring one sometimes disfavor the other. Thus it is advantageous for the individual to remain a unit as long as possible and to keep all of its parts integrated closely into the one unit; but if this were done there could be no reproduction of new individuals, for new individuals are produced by the isolation of parts of the parent. Some types of reproduction entirely disrupt the parent organism, the whole parent body going into offspring, but in other types of reproduction only relatively insignificant parts of the parent go to form offspring and the parent lives on for a time.

It often happens, however, that reproduction marks the end of the life of the individual and there are many instances in which individual is sacrificed for the good of the race. Commonly, hard conditions in the environment injure the individual but favor reproduction. The individuals perish, but the race is saved. Even among the lower animals parents give up their lives to save their offspring. We need not further elaborate this principle here, for we shall encounter illustrations of it in subsequent chapters.

C. An Attempt to Classify Organic Mechanisms

For the sake of clarifying our treatment of the mechanisms of life we offer the following classification:

I. Mechanisms of Individual Maintenance and Adjustment.

1. Nutritive Mechanisms.
2. Integrating and Coördinating Mechanisms.
3. Mechanisms of Individual Adjustment to Changes in the Environment.
4. Special Adaptations of the Individual to the Environment.

II. Mechanisms of Racial Maintenance and Adjustment.

1. Modes of Reproduction.
2. Germ Cells and Their Origin.

3. Evidences of Organic Evolution.
4. Variation and Heredity.
5. The Causal Factors of Organic Evolution.

In the remaining chapters of the book we shall follow the organization given above without further explanation as to the logical development of the sequence of topics.

SUMMARY

1. Living and lifeless mechanisms have some fundamental similarities, but differ in several important respects. A lifeless mechanism is incapable of growth and repair, cannot reproduce offspring, cannot start, stop, or change the rate of its own activities, and cannot change itself in adaptation to its environment.

2. An organic mechanism is regarded as a complex integrated unit in which all activities are due to changes of matter and energy. Some of the activities of higher organisms may be due to matter and energy changes that are different in kind from any exhibited by lifeless mechanisms and therefore are peculiar to the levels of unity which we call intelligent beings. These activities are nevertheless natural in that they are expressions of matter and energy changes at very complex levels of unity.

3. The various mechanisms found in organisms may be classed in two categories: *a*, those favoring individual maintenance and adjustment, and *b*, those favoring racial maintenance and adjustment.

4. Individual welfare and racial success are not always compatible. In fact, there is often antagonism between these two "objectives." What is best for the individual is not always good for the race, and *vice versa.*

CHAPTER XXXVIII

NUTRITIVE, MAINTENANCE, AND GROWTH MECHANISMS

(A BRIEF SURVEY OF HUMAN PHYSIOLOGY)

A. General Statement

In those chapters dealing with various types of animals and in those dealing with the energy traffic and the chemical composition of protoplasm a good deal has been said about processes of energy expropriation, foods, digestion, respiration, egestion, and excretion. In the chapter on *General Physiology of the Frog*, moreover, we have covered the ground contemplated in this chapter in a somewhat superficial way. Because of the fact that these subjects are not new it would seem to be a good plan to add something novel and valuable, and at the same time introduce something of especial human interest. We shall therefore bring man into the picture and deal in this chapter exclusively with HUMAN MECHANISMS. By comparing what we shall now present with what has been said about other organisms we should gain the impression that there is a vast deal in common between man and his fellow animals.

B. Foods

Man is an omnivorous animal subsisting upon a much more varied diet than do most other animals. Like other animals, he must secure for the maintenance of his cellular constituents all the basic building stones for his own special proteins and all of his fuel stuffs from the materials already manufactured by plants or from the bodies or products of plant-eating animals. Man requires not merely a certain quantity of food but a considerable variety of special food ingredients.

Man's food consists of the following classes of materials:

1. Proteins
2. Carbohydrates
3. Fats

4. Inorganic salts
5. Vitamines
6. Water

1. Proteins.—As has been explained in Chapter VII, the protein molecule is very complex in structure, consisting of amino-acid building stones. Human proteins are of very many sorts and contain numerous amino-acids combined in various combinations. Since neither man nor any other animal can manufacture amino-acids, it stands to reason that he must use for foods proteins that contain sufficient of each of the kinds of amino-acids necessary for the elaboration of his own specific proteins. This means of course that he must use protein foods of many sorts, for no one type of food protein contains all the amino-acids required. Plant proteins alone, if of sufficient variety and amount, would furnish the necessary amino-acids, but many common plant foods are rather poor in proteins. Animal flesh (lean meat) is more nearly adequate, but any one kind of meat also lacks some essentials. Casein, the protein of milk, is very rich in some necessary amino-acids. There are still other valuable amino-acids in hen eggs. The dietetic lesson to be derived from these facts is that one should use as wide a variety of proteins as can be obtained, always considering the capacity to digest and special sensitivity of the individual to particular proteins, for there are wide ranges of difference in individuals in these respects. Also the quantitative protein requirements of individuals vary and they vary in the same individual under different conditions of health and activity. Any extensive discussion of these matters would lead us too far afield.

2. Carbohydrates.—The food carbohydrates consist of sugars and starches of which there are many different kinds. There seem to be no qualitative differences among the sugars and starches so far as specific requirements are concerned. The only difference seems to be a matter of digestibility. The carbohydrate requirement varies with the individual, the average adult requiring about 2500 calories a day. The physiological calorie is the unit measure of energy content in food, a single calorie being that amount of energy required to raise the temperature of a liter of water one degree, Centigrade. Carbohydrates, as has already been pointed out, are primarily fuel foods, though to some extent they enter into the structural make-up of cells. They are either

promptly burned in the cells or else are stored for various periods in the tissues. In plants the storage form of carbohydrates is STARCH, in animals it is GLYCOGEN (animal starch), stored chiefly in the liver and in muscles. In animals glycogen may be compared to a checking account in the bank, a reserve fund to be drawn on for current uses whenever the funds in actual circulation run low.

3. Fats and Oils.—These lipoid food materials are derived from both animal and plant sources. Once more, there appears to be no marked qualitative difference as to food value except rather striking differences in the digestibility of different fats. Fats eaten in large quantities tend to interfere with the digestion of other foods in the stomach, for they are likely to form oil films about particles of proteins that interfere with the penetration of gastric juices at the proper time. Fats may be either burned at once or stored. When stored they may be compared to a savings account in a bank, a reserve not to be drawn upon for current needs, but only when the sugar and glycogen in the system becomes depleted through prolonged exertion or starvation. Excess sugar is commonly converted into fat and stored in adipose cells. Fats may be broken down when needed to form sugars. Excess proteins are also broken down, the nitrogen fraction being converted by the liver into urea, which is excreted by the kidney, while the rest of the molecule may be converted into fat.

4. Inorganic Salts.—The importance of a proper balance of inorganic salts in the blood and in cells has already been emphasized. It is obvious that the human body must have the proper amount and variety of salts in its food. The *average* daily salt requirement for a human adult is as follows:

Calcium, $1\frac{1}{2}$ to 2 grams (of the oxide)
Phosphorus, $\frac{1}{2}$ to 1 gram
Iron, about $\frac{1}{20}$ of a gram
Sodium chloride, 5 grams.

Traces of other salts are essential, but it is not necessary to receive them every day. These salts are usually present in sufficient amounts in ordinary food and in natural water. Rich sources of the more important salts are meat, milk, eggs, whole grain, and vegetables. The body responds in various unfavorable ways whenever there occurs a calcium deficiency, a phosphorus or an iron deficiency. Rarely is there a sodium deficiency. Since the inorganic salts are soluble in water no special digestive process is

required to enable them to pass through cell membranes and to enter the blood stream.

5. Vitamines.—These are foodstuffs of somewhat recent discovery, but they have not lacked for publicity. They are natural substances present in our foods, but very little is known as to their chemical nature. That they are not important as energy sources is indicated by the minute quantities necessary for bodily well-being. The various vitamines are known as A, B, C, D, E, and F, because they have not been chemically analyzed and it is difficult to give them significant names. They are, however, sometimes named after the kind of abnormal condition that appears in the body when they are absent or deficient—as the antiscorbutic (antiscurvy) vitamine C and the antirhachitic (antirickets) vitamine D. The letters used to designate the vitamines also indicate the order of their discovery, A being discovered first and F last of those listed.

The following are the chief vitamines that have been discovered by feeding tests on laboratory animals:

Vitamine A.—Deficiency in various degrees results in impaired growth and maintenance, increased susceptibility to many infections, a morbid condition of the eyes, and death if not corrected.

Vitamine B.—Its absence produces the disease "beriberi," whose symptoms are nerve degeneration, retarded growth in young individuals, loss of appetite, and death if not corrected.

Vitamine C.—Lack of this substance in the food causes "scurvy." This serious disease used to be common among sailors on long voyages and among city inhabitants during sieges. The symptoms of the disease are hemorrhages of joints and disorders of the teeth and gums. It may be fatal if not controlled. Most fresh fruits and vegetables contain vitamine C, and the prevention or cure of scurvy consists of merely eating plenty of the latter.

Vitamine D.—Its absence or serious deficiency causes "rickets" in infants, a disease involving improper bone and tooth formation and resultant deformities. Though not necessarily fatal, these conditions are serious. Exposure to sunlight seems to be a good substitute for vitamine D, for reasons explained below.

Vitamine E.—This might be called the "fertility" vitamine, for its absence seems to be associated with no other symptom than reproductive infertility. Feeding the vitamine restores individuals to normal fertility.

Vitamine F.—This has been called the "pellagra-preventing" vitamine. The disease, formerly common among the "sow-belly, corn-pone" population of our Southern States, is corrected by adding to the limited diet fresh vegetables of various kinds.

The vitamines are widely distributed and abundant constituents of such common natural foods as milk, butter, cheese, eggs, whole grain, fresh vegetables, citrous fruits, and the fats and oils of fish, fowls, and beef. There is very little danger of vitamine deficiency for anyone who partakes of a mixed diet of the usual sort. In the winter time, however, when the ultra-violet rays of sunlight are diminished for various reasons, one should make an effort to increase his vitamine supply by the use of foods rich in vitamines, especially vitamine D, which is abundant in fish oils, such as cod-liver oil or similar substances. In the summer, when plenty of ultra-violet rays reach us, moderate exposure of the skin to direct sunlight causes some of the animal fats near the surface of the skin to produce or release vitamine D in sufficient amounts.

The investigation of vitamines has involved the use of many sorts of laboratory animals and illustrates the scientific method. Litter mates (offspring of the same parents born at the same time) are divided into two equal lots, one (the control) fed on normal rations, and the other on a ration containing everything in the normal ration except the particular vitamine under investigation. Any symptoms appearing in the experimental group that do not appear in the control may then safely be attributed to lack of the particular vitamine in question.

6. Water.—As a food, water is of course one of the most, if not *the most*, essential ingredients of our diet. While a human being can survive for a long time without food, he will live only a relatively short time without water. Since protoplasm is composed so largely of water, partial desiccation interferes seriously with all bodily processes.

C. Digestion, the Splitting of Complex Molecules into Simple Ones

Two aspects of digestion deserve especial attention: *a*, the highly specific character of the chemical changes activated by particular enzymes, and *b*, the delicate timing and coördination of the various steps in digestion.

The function of digestion, as we have said before, is that of

breaking down molecules too large to pass through cell membranes, into molecules small enough to pass through them. The foods that are made up of large molecules are proteins, fats, and carbohydrates. The chemical breakdown of each of these is facilitated by an elaborate mechanism involving mechanical, chemical, and nervous activities beautifully coördinated. In our account of digestion in the frog the various digestive organs and their functions were dealt with, but no account of the sequence of events in digestion was given and nothing was said about the mechanisms of coördination and control. In this account we shall follow the course of digestion of an ordinary mixed meal as it goes on in any one of us, and shall emphasize the coördinating mechanisms involved.

a. Digestion in the Mouth.—The first step in digestion is *mastication*, a voluntary mechanical process resulting in the grinding up of larger masses into smaller masses, thus exposing a larger surface area to the action of digestive juices. The degree of completeness of mastication varies with the individual and is a matter of habit.

Mastication is accompanied by the secretion of SALIVA, a viscous, colorless fluid secreted by SALIVARY GLANDS, whose ducts empty into the mouth cavity. Saliva consists of mucus, which acts as a lubricant that facilitates swallowing, and an enzyme, PTYALIN, which aids in the chemical splitting of starch into sugars. This process does not occur to any great extent in the mouth, for the food does not remain very long there, but takes place largely in the stomach. The secretion of saliva is a good example of a simple reflex act. Nerve end-organs both in the taste buds and in the olfactory epithelium are stimulated by the taste or smell of savory food. Nervous impulses from these sensory cells are conducted to nerve cells in the brain which automatically send secretory impulses to the salivary glands, inducing discharge and further elaboration of saliva.

After mastication comes the act of swallowing. The first step in swallowing a food bolus is voluntary and involves the closing of all openings into the mouth except that into the gullet. Then by suddenly contracting all the muscles of the mouth cavity, food is squeezed through the only available opening into the top of the œsophagus. After the food once enters the œsophagus its further progress is involuntary. It is carried downward to the stomach

by successive waves of peristaltic muscular contractions, which proceed, normally, only in one direction.

b. Digestion in the Stomach.—The stomach is a greatly enlarged, highly muscular expansion of the digestive tract. The cavity or lumen of the stomach is at all times adjusted to the amount of food in it. When no food is present there is no true lumen. The entrance of food is made possible by a relaxation of the muscles in the stomach wall and is controlled by another type of reflex action. When the stomach is well filled with food it becomes virtually a closed sac due to the contraction of strong sphincter muscles both at the point of entrance of the œsophagus and at the point where the stomach joins the small intestine. Now begins the process of stomach digestion, which may be likened to a churning process. Strong waves of contraction proceed from one end of the stomach to the other, squeezing the food back and forth. This is of course a purely mechanical process similar to mastication, but while this is going on the food is thoroughly mixed with a digestive fluid, GASTRIC JUICE. This second digestive secretion is poured into the stomach from thousands of tiny glands in the lining of the stomach. The colorless fluid, gastric juice, contains HYDROCHLORIC ACID and a digestive enzyme, PEPSIN, which in the presence of an acid takes the first step in splitting up proteins. The secretion of gastric juice is regulated by two mechanisms, nervous reflexes and hormonal action. While the food is still in the mouth nerve-endings in the mouth lining conduct impulses to the brain (medulla) where other nerve cells, picking up the impulse, relay it automatically to the nerve-endings in the gastric glands, causing them to secrete a good supply of juice prior to the arrival of food in the stomach. The preliminary gastric secretion is sometimes called "APPETITE JUICE." Unsavory food does not adequately excite the production of appetite juice and its digestion may thus be impeded. Another automatic regulator of gastric digestion consists of the secretion of GASTRIN, a hormone produced in the stomach walls under the stimulation of food substances in the stomach. This substance is taken up by the blood and carried to the gastric glands, which are stimulated thereby to secrete more gastric juice.

When the stomach has finished its job, the food is, normally, in a fluid condition somewhat like milk in consistency and appearance, and is then known as CHYME. This is distinctly acid in reac-

tion. During stomach digestion the starches have been partially split up into sugars through the action of ptyalin and the proteins have been split into intermediate fractions, proteoses and peptones, and some have been reduced to amino-acids.

c. Digestion in the Small Intestine.—When the food has been reduced to chyme the pressure of the stomach contraction overcomes the constricting action of the pylorus muscle that has hitherto closed off the stomach from the intestine, and the chyme is squirted little by little into the duodenum (the upper end of the small intestine), where it is at once mixed with three more digestive secretions, pancreatic juice (from the pancreas), bile (from the liver), and intestinal juice from glands lining the intestine, the action of which completes the chemical splitting of materials whose digestion was begun in the stomach.

PANCREATIC JUICE is a clear watery solution, alkaline in reaction, composed of inorganic salts and three enzymes, TRYPSIN, STEAPSIN, and AMYLOPSIN. The secretion is produced by glands in the pancreas and poured into the intestine through the pancreatic ducts. The regulating mechanism responsible for the secretion of pancreatic juice is much like that of gastrin, mentioned in the case of gastric secretion. The presence of acid chyme stimulates the cells lining the intestine to produce a hormone, SECRETIN, which is given off into the blood and is carried to both pancreas and liver, where it stimulates them both to secrete more of their respective juices. When the acidity of the food mixture is neutralized by the alkalis in the pancreatic juice, secretin is no longer released and the pancreatic secretion slows down to the level present between meals.

The three enzymes of the pancreatic juice (trypsin, steapsin, and amylopsin) perform different and separate functions in digestion. Trypsin still further splits up the partially split proteins but does not quite finish it; steapsin splits up the fats (which have been emulsified or changed into soaplike materials by the bile); and the amylopsin completes the breakdown of starch into simple sugars, a process begun by ptyalin.

BILE, the secretion of the liver is secreted at all times, but between meals is stored and concentrated in the gall bladder. During the digestive process it is emptied in considerable quantities into the small intestine. Its main digestive function is that of making a soapy emulsion of the fats, thus rendering their splitting by steapsin much easier.

Intestinal juice (succus entericus) is secreted by the gland cells lining the small intestine. It contains an enzyme, erepsin, whose function it is to finish the job of splitting whatever residue of protein fractions remain incompletely split, reducing them completely to amino-acids.

The mechanical feature of intestinal digestion is similar to that in the stomach. Waves of peristaltic muscular contraction continuously pass through the walls of the intestine squeezing and spurting the fluid food back and forth and thoroughly mixing it with all the juices.

When the food is sufficiently split up into relatively small molecules these pass by diffusion and osmosis into and through the cells lining the cavity of the small intestine. In this way the nutritive elements reach the blood or the lymph and are in a position to be transported to the ultimate consumers, the cells all over the body.

The undigested or indigestible residue passes into the large intestine where it is concentrated and is finally packed in the rectum ready for elimination. When the food residue reaches the large intestine it is of the consistency of thick cream, but it is rendered progressively more solid through absorption of water by the walls of the large intestine.

This whole intricate and beautifully coördinated process may, of course, be upset by various means. A failure of any of the mechanisms involved may easily disrupt the process and indigestion, slight or severe, may result. Such a delicately adjusted series of processes might be expected to be readily disturbed by emotional excitement, by fatigue, and by disease, but this is hardly the place to discuss the pathologic aspects of digestion.

D. Circulation, Assimilation, and Excretion

The physiology of these three processes is so complex and difficult to understand that we shall deal with it only in very general terms.

Circulation may be regarded as a very important integrating or coördinating mechanism and as such should perhaps be left for the next chapter, but will be considered here for obvious reasons. From the standpoint of its rôle in nutrition we need merely point out that circulation serves to distribute the very complex mixture of digested food materials all over the body and to give them up to whatever cells are in need of them. Some cells take up some materials; others take up other materials. Thus

there is a selective absorption or sorting out of the numerous special substances. The blood and the lymph are the circulating media. The blood contains representatives of almost everything produced by body cells except the structural materials of the cells themselves. The blood may be regarded as the internal environment of the cells and must therefore be very definite in its composition and concentration.

The motive power of circulation is the heart aided by the arteries. The blood is forced under pressure through a complete circuit of blood vessels. The blood pressure is modified by both nervous and hormonal regulators which increase or decrease the rate of heart beat and cause constriction or dilitation of the arteries. It may be increased or decreased locally as the need for more or less blood changes in various parts. No more beautiful example of a complex and nicely coördinated mechanism could well be mentioned than that which controls blood pressure.

Assimilation is that process in which the individual cells select the materials they need to supply energy for cell life or for growth or repairs of cell structures. Oxygen is, of course, carried in the blood and this oxygen is used to burn the fuel ingredients received from the blood. In this sense oxygen is a food. The blood picks up oxygen by means of its red blood cells in the capillaries of the alveoli of the lungs. The by-products of combustion of carbohydrates (H_2O and CO_2) are given off into the blood and discharged, the water through the kidneys, sweat glands, and lungs, and the carbon dioxide through the lungs. This process is known as excretion and should not be confused with that of elimination of indigestible solids from the rectum. When proteins are combusted in the cells some of the by-products are carried to the liver where they are converted into urea, which is excreted in large quantities by the kidneys. The kidneys also help to regulate the concentration and proportion of the various inorganic salts in the body, thus helping to render the chemical composition of the blood nearly constant.

We have traced the raw materials of nutrition from their source to the ultimate consumers, the living cells, and have given a suggestion as to how the cells use them and how they get rid of their waste products. One will doubtless be impressed by the fact that, by and large, man carries on the same sort of energy traffic as do other animals.

SUMMARY

1. In this chapter is given a brief survey of some of the most important aspects of human physiology, especially those that have to do with nutrition, maintenance, and growth.

2. Man is omnivorous and must get all his energy from foods. These foods must supply at least the "building stones" for maintaining and restoring all the special materials of which his protoplasm consists. Hence, the list of human foods is about the same as is that of the chemical constituents of protoplasm: proteins, carbohydrates, fats, inorganic salts, water.

3. Vitamines are food substances that do not enter into the structure of protoplasm as such, but are essential for normal life.

4. Proteins are the most complex substances used as food. A considerable variety of different proteins are required to furnish all the amino-acid "building stones" necessary to produce human protoplasmic proteins. Proteins are used mainly for maintaining and restoring the structural groundwork of protoplasm.

5. Carbohydrates are much less complex than proteins, though starches and complex sugars are composed of many "building stones" (molecules of simple sugars). Carbohydrates, though entering somewhat into protoplasmic structure serve mainly as fuel, or as sources of energy for current living.

6. Fats are important ingredients of cell membranes and of other parts of cells. In addition, they are very valuable as storage materials to be called into use only if carbohydrates run low. Carbohydrates can be converted into fats and *vice versa.*

7. Inorganic salts of certain definite kinds and in certain definite amounts are necessary ingredients of food, for they must be present in the blood and in tissues in a very constant ratio to each other. The ions resulting from the electrolysis of molecules of salts play a very important rôle in regulating the energy traffic within cells.

8. Vitamines are natural food stuffs of unknown chemical composition found in combination with various other food substances. A deficiency in any particular vitamine results in certain specific morbid symptoms. Deficiency in vitamine A results in impaired growth; in vitamine B, beriberi; in vitamine C, scurvy; in vitamine D, rickets; in vitamine E, sterility; in vitamine F, pellagra.

9. Water is essential as a solvent for the ingredients of protoplasm, which is made up largely of substances in aqueous solution.

10. Digestion, which consists of the splitting up of large molecules of foods into small molecules, is a complex process involving mechanical processes controlled by reflexes, chemical processes facilitated by organic catalysts (enzymes), and chemical messengers (hormones). These all work in a coördinated fashion so that each part of the process occurs at the proper time.

11. The main reflexes have to do with: the production of saliva, the production of appetite juice, the movements of the œsophagus in swallow-

ing and of the stomach and intestines in churning the food mixture, the opening of the stomach valves, etc.

12. The main enzymes involved are ptyalin of the salivary glands, pepsin of the stomach, trypsin, steapsin, and amylopsin of the pancreas, and erepsin of the intestine, each of which carries out a specific rôle in the splitting of food molecules.

13. The chief hormones involved in digestion are gastrin and secretin, the former regulating the amount of gastric juice secreted and the latter the amount of pancreatic juice and bile that are emptied into the intestine.

14. Bile is not a true digestive juice, but it changes fats into soaps and thus renders them digestible by steapsin.

15. Circulation involves the distribution of digested food to the cells, the ultimate consumers.

16. Assimilation is that process going on in the cells involving the use of food materials for respiration (release of kinetic energy) and the building up of more structural parts of the protoplasm.

17. Excretion is the giving off of the by-products of complete or partial oxidation. Excretory products, such as CO_2, H_2O, and urea are eliminated by lungs, skin, and kidneys. As compared with foods, excretory products are very low in potential energy.

CHAPTER XXXIX

INTEGRATING AND COÖRDINATING MECHANISMS

A. General Statement

As has already been pointed out, the most important fact about life units is that the complex components of the unit, be it a single cell or a many-celled organism, are so organized that the unit behaves as a whole. In the simpler units the unifying or integrating mechanisms are relatively simple, but as the organisms become very large and complex additional mechanisms of coördination and integration come into play. In general, it may be said that the more complex the organism, the more the need for special integrating mechanisms.

There seem to be three main types of integrating mechanisms: *a*, Physiological gradients, *b*, Chemical (especially hormonal) mechanisms, and *c*, Nervous mechanisms.

B. Physiological Gradients

In dealing with the various animal types reference has been made on several occasions to special applications of ***Child's*** METABOLIC GRADIENT (OR PHYSIOLOGICAL GRADIENT) THEORY and some of its implications. Child's theory attempts to explain in dynamic terms various outstanding aspects of organization, common to most life units, such aspects as polarity and symmetry. We have long recognized that cells are organized about an axis and that the two poles of the axis differ, the so-called upper pole being called the animal pole and the so-called lower pole, the vegetal pole. Some cells, especially the eggs of animals having determinate cleavage, have dorsal and ventral surfaces and even exhibit bilateral symmetry. It has also been realized for a long time that most multicellular animals are organized on a similar plan. We speak of the anteroposterior axis of vertebrates, arthropods, etc., of the dorsoventral or ventrodorsal axis of the vertebrates and arthropods respectively, and of the symmetry axes of various sorts exemplified by different groups. These axes have long been recog-

nized as very fundamental features of the structural organization of animals in general, but it remained for Child to interpret these obvious morphological features in physiological terms.

The theory of physiological gradients is a very elaborate one and we shall have to be satisfied merely to outline some of its salient features. Since the physicochemical nature of the primary axis, or axis of polarity, is essentially the same as that of the secondary axis, the axis of symmetry, we shall limit this discussion to the axis of polarity. The polarity of simple life units such as cells and at least the simpler metazoan animals such as cœlenterates and flatworms, is believed to be due to the existence of a gradient of physiological activity running from pole to pole of the axis. That end of the axis known morphologically as the animal pole of egg cells and the anterior end in simple Metazoa is regarded as having the highest rate of metabolic activity in the whole unit. Proceeding downward along the axis there is a gradient of gradually decreasing metabolic rate which reaches its lowest point at the end of the axis farthest from the high point. Child uses the terms APICAL END for the high point and BASAL END for the low point. He believes that "the foundations of unity and order in the organic individual is the transmission of dynamic change, 'stimulus,' 'excitation,' from one point to another in the protoplasm." The apical end, having the highest rate of metabolism, sends waves of stimulation down the axis, each higher metabolic level transmitting the stimulus to the next until it reaches the basal end. As the stimulus passes down the axis it diminishes in intensity and in large organisms it may fade out before it reaches the parts most distant from the apical end. It is because of this that, in complex organisms, additional integrating mechanisms are necessary in order to maintain unity.

The apical region may be regarded then as the dynamic "head" of the organism. The principle of control may be likened to that which obtains in a great business organization. Any well-integrated business organization has one head, the director or president, from whom all orders emanate. His orders are passed on to subheads or department heads, who pass them on to the next in rank until they finally reach the lowest workers. The more powerful and dominating the head of the organization is, the more coördinated and integrated the business organization becomes.

In like manner, individuality or unity in organisms depends on

unified control. The individual is a unit because it has a controlling center from which emanate the integrating stimuli. The validity of this, as of any theory, depends on evidence. The experimental work that gave rise to the theory is very extensive. One type of evidence consists of demonstrations that there is a metabolic gradient in many kinds of organisms. The essential feature of metabolism is the oxidation of materials in the cells resulting in the production of by-products such as carbon dioxide. It has been shown for various kinds of cells and in some of the simpler metazoan organisms that the rate of oxygen consumption and that of CO_2 production is highest at the apical end and decreases steadily down the axis. Methods of measuring metabolic rate are many and ingenious. Perhaps the crudest method is that of cutting an elongated animal like a planaria into several pieces representing different levels of the axis (Fig. 131). If a hundred *A* pieces, a hundred *B* pieces, and a hundred *C* pieces are placed in equal amounts of water with equal amounts of oxygen in solution and are allowed to live in the water for some hours, it should be possible to measure the relative amounts of oxygen used and CO_2 produced by the three lots of one hundred pieces. By sensitive instruments it is found that *A* pieces use the most oxygen, *B* pieces less, and *C* pieces least. Similarly CO_2 production is highest in *A* and lowest in *C* pieces.

Another method less objectionable than the first, since it does not involve cutting up the animals, is called the SUSCEPTIBILITY METHOD, the basis of which is as follows: A part of an organism in which the metabolic rate is highest requires most oxygen to keep up its normal life processes, and that with the lowest metabolic rate requires the least oxygen. Deprivation of oxygen will first be felt by the apical region and last by the basal region. Now certain chemicals kill tissues by preventing cell respiration, and when an organism such as Planaria is placed in a solution of such substances it can be seen to die and begin to disintegrate first at the anterior end and then a death wave proceeds down the gradient.

Another method of detecting the metabolic gradient is by means of color changes in certain chemicals. Methylene blue is a substance which contains much oxygen in a rather loose state, so that other substances in need of oxygen can take it away and leave the methylene blue in a reduced condition in which it is

colorless. When a planarian is immersed in a solution of methylene blue, which is relatively harmless, the animal is stained blue all over. When removed from the solution, however, the tissues of the worm begin to use the loosely bound oxygen of the chemical and there is a progressive fading out of the blue color. The head parts are the first to lose color and a wave of decoloration proceeds steadily down the axis, the basal region being the last to lose color.

These and many other experiments seem to demonstrate the existence of metabolic gradients. It is difficult to quarrel with the facts, but many biologists disagree with the interpretation that Child and his co-workers have placed on these facts. In the opinion of the writer, the general principles involved are valid and deserve a heartier reception than they have received in some quarters.

Now the integrating mechanism involved in the gradient mechanism seems to be effective of itself only in relatively small organisms or during embryonic stages of larger and more complex organisms. Apparently the mechanism of transmission of stimuli through the protoplasm from the apical region has certain spatial limitations. It is effective only over relatively short distances. Parts distant from the apical region in larger animals and older embryos seem to get partially or completely out of control and to start new gradients of their own. This would result in disintegration and loss of unity were there not reinforcing mechanisms of integration.

C. Chemical Mechanisms of Integration—Hormones

While there are numerous chemical activities involving the interaction of the various inorganic salts and those of protein molecules, etc., the most interesting and striking chemical agents of coördination, regulation, and integration are the so-called HORMONES, the specific products of the ductless glands or the glands of internal secretion (ENDOCRINE GLANDS). While there may be endocrine glands among other animals, they are especially characteristic of vertebrates. We have already seen how certain hormones help to regulate and harmonize the digestive processes. The hormone GASTRIN was shown to regulate the secretion of gastric juice and the hormone SECRETIN to regulate the secretion of pancreatic juice and bile. In both cases these hormones help

materially to coördinate the different stages of the whole elaborate digestive process.

The study of ENDOCRINOLOGY is one of the most active phases of modern biology. The functions of many endocrine glands are still incompletely understood, but there is no question as to their fundamental importance in regulating and integrating the physiological processes of the whole organism. Some of the most important endocrine glands are to be regarded as in a sense vestigial organs, as the transformed remains of organs that had quite a different function in the ancestors of the higher vertebrates. Thus the important THYROID GLAND is regarded as a vestige of the endostyle of the chordate ancestor, the PARATHYROID GLAND of one of the former gill pouches, the HYPOPHYSIS as possibly a relict of the primitive mouth of early chordate ancestors. Even though these may be considered as vestiges of the past, they have acquired new functions that make them absolutely indispensable in the maintenance of life.

The THYROID GLAND in man is a rather large gland situated in the neck, located just posterior to the larynx on the two sides of the windpipe. It is the gland that enlarges abnormally in persons with one kind of goiter. This gland gives off into the blood a hormone known as THYROXIN, the active principle of which is iodine, an element that makes up about 65 per cent by weight of the thyroxin molecule. Disturbances in thyroxin production may result either from iodine deficiency in the food or from a failure of the thyroid gland to synthesize the hormone.

In normal individuals the rate of general resting bodily metabolism is rather constant. Tests are made that give us a measure of metabolism known as the BASAL METABOLIC RATE. The secretion of the thyroid gland is largely responsible for maintaining a normal and constant metabolic rate. It is primarily a metabolism regulator for the whole body. If, because of too little iodine in the food or inadequate functioning of the gland, too little thyroxin is poured into the blood, marked effects on growth, development, and normal functioning of the body result. If the deficiency is present in infants the result is known as CRETINISM. The CRETIN is a repulsive dwarf, pot-bellied, with malformed features and limbs, and subnormal mentality. If thyroxin is administered early enough almost miraculous improvement sometimes results: the monster sometimes becomes practically normal. In older persons

thyroxin deficiency results commonly in enlargement of the gland (an apparent attempt on the part of the organ to compensate for its poor quality by increased quantity), the basal metabolism drops, myxodema (accumulation of water in tissues), sluggishness physically and mentally, and other symptoms appear. These may be partially remedied by thyroxin administration.

It has been noticed that goiter has a peculiar geographic distribution, being most prevalent in regions far from the sea and rare along sea coasts. This is thought to depend upon the relative scarcity of iodine in soil and water in mid-continental regions and its relative abundance in the sea and near the coast. Sea foods contain iodine, and the closer to the sea people live, the more are sea foods used.

Thyroxin may also be produced in excess by the thyroid gland, and a condition of hyperthyroidism results. This disease is far more common among women than men. Its symptoms are greatly increased basal metabolism, too rapid oxidation of tissues, marked nervousness, rapid pulse, protruding eyeballs, etc. Unless relieved by removal of the proper portion of the gland, death usually results.

In lower animals thyroxin plays a very striking rôle in developmental crises such as the metamorphosis of amphibia (see pp. 430–431). Removal of the thyroid gland from young tadpoles causes them to remain in the larval state all their lives, but feeding them on thyroid causes them promptly to metamorphose. In some species, such as the northern bullfrog, which requires three or four years to reach the time for metamorphosis, young tadpoles of the first year may be caused to metamorphose prematurely by thyroxin administration.

The thyroid gland regulates the activity of all other endocrine glands, but some of the latter, notably the HYPOPHYSIS, exercise a reciprocal regulating influence upon the thyroid. In general, it may be said that the endocrine glands work together, acting as brakes and checks upon one another, thus insuring unity and coördination of action among themselves.

A second hormone of great significance is INSULIN, which is secreted by the "islet" cells of the pancreas. Insulin secreted directly into the blood regulates the quantity of blood sugar. Its function is that of facilitating the oxidation of sugar in the tissue cells. If, as in the disease DIABETIS MELLITUS, the islet glands secrete too little insulin, excess sugar accumulates in the blood and

is excreted in the urine. The result is that the tissues are deprived of the necessary fuel for energy production and serious ill health results. In severe cases death ensues unless the condition is relieved by injections of insulin. One of the foremost contributions to medical practice in recent years was the isolation by ***Banting*** in 1922 of pure insulin, using as material pancreas tissue of food animals. This discovery has been of great benefit to untold numbers of suffering human beings. The work could not have been carried on successfully, according to a statement of Banting himself, except by the use of dogs as experimental animals. Were physiologists denied the use of superfluous dogs from the pound for investigations such as this, human suffering would be greatly increased.

The PITUITARY GLAND (HYPOPHYSIS) is a tiny gland near the base of the brain that secretes a number of essential hormones, each of them having a different regulatory function. Because of its effects on various other glands as well as its direct effects on growth it has been called the "master gland." Insufficient pituitary secretion in young individuals results in infantilism, or permanent infancy. Growth ceases early and sexual maturity is inhibited. On the other hand, excess activity of the pituitary in infants sometimes results in very precocious sexual maturity and other deleterious conditions. When the hyperactivity of the gland comes in later life, gigantism is one of its results. "Pituitary giants," as they are called, usually are characterized by excess bone growth, the hands and feet being extremely large, the jaw and face bones very massive and joints disproportionately large. The pituitary gland also controls and conditions the growth, maturity, and rhythmic activities of the sex glands. This subject is, however, a very complicated one and need not be elaborated further.

The rôle of the OVARIES and TESTES as endocrine glands, in contrast with their rôle as organs in which germ cells are produced, has received a great deal of attention during the last decade. The effects of both testicular and ovarian hormones upon the growth and differentiation of the secondary sex characters is well known. For example, the difference between the rich and elaborate plumage, head furnishings, and other features of the brown leghorn cock, and the contrastingly plain characters of the hen of the same breed, is accounted for by the difference in hormones. If the ovary

of a young pullet be completely removed, the bird will develop plumage and head furnishings fully as fine as those of a cock, indicating that in the normal hen the ovary secretes a hormone that inhibits the development of the full specific plumage.

In mammals, such as rats, mice, guinea pigs, and others, the removal of the ovaries or testes from young animals prevents the development of the adult male or female secondary sexual characters, and the animal remains permanently juvenile or neutral. If, however, into a young animal from which the testes have been removed, a piece of ovary be introduced in such a way as to enable the latter to survive and grow, the animal will be more or less altered in a female direction. This shows that an individual genetically of one sex may be modified in the direction of the other sex by means of hormones.

A beautiful experiment conducted by nature herself helps to make the function of the sex hormones quite clear. *Professor F. R. Lillie* has shown that, in cattle, twins occur in a small percentage of births and they come from two fertilized eggs, usually one egg coming from each ovary. As a rule, the two eggs develop in opposite horns of the two-branched uterus. Each embryonic vesicle grows excessively long and both extend down into the unpaired median portion of the uterus, where they come in contact and usually undergo more or less extensive fusion of their chorionic membranes. One sequel of this fusion of embryonic membranes is that the blood vessels of the two fetuses fuse, or anastomose, and the blood streams of the two individuals become mixed. The result of this admixture of fetal blood is as follows:—If both individuals of the pair are of the same sex no harm is done, but if they are of opposite sexes the female is always the one to suffer. She becomes profoundly modified in a male direction in all secondary sexual characters. Farmers have long known of these anomalous individuals and have called them FREEMARTINS (Fig. 230).

The explanation offered for this result is as follows:—The male gonads (testes) differentiate very early in fetal life, while the female gonads (ovaries) differentiate much later. At the time when the blood streams of the two individuals mingle, the only sex hormone in circulation is the male hormone. The prospective female individual then comes under the controlling influence of the male hormone and is acted upon in such a way that the whole future

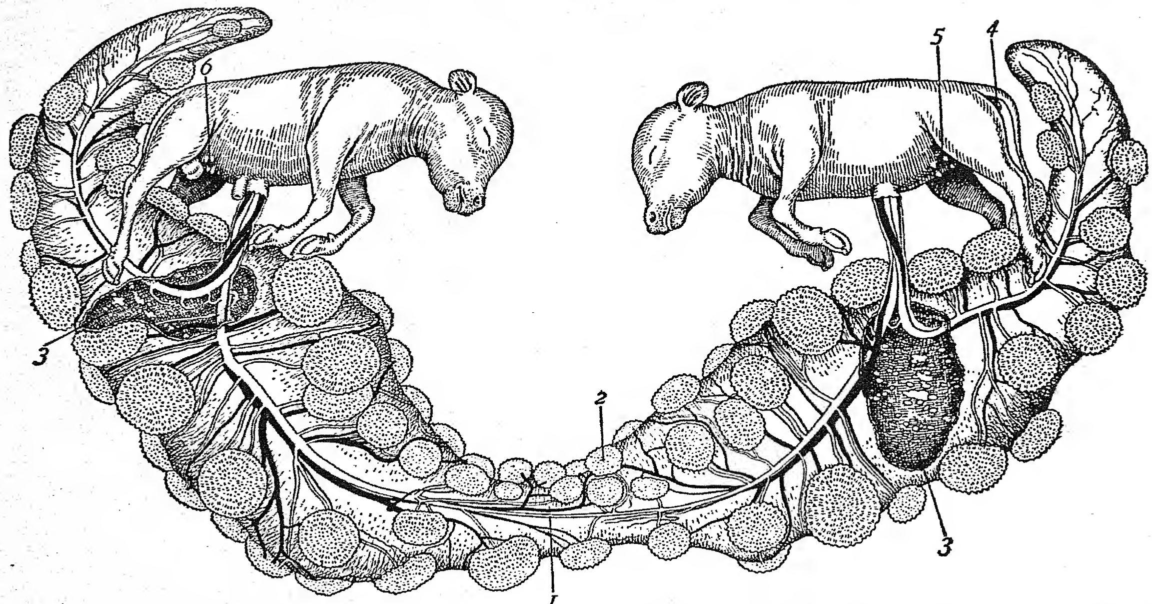


FIG. 230. A typical opposite-sexed pair of cattle twins, male on the left and freemartin on the right, showing: *1*, the connecting artery between the two twins; *2*, a single placental cotyledon entered by veins from both fetuses; *3*, opening into the chorion through which the fetuses have been removed; *4*, clitoris of the freemartins; *5*, the well-separated anterior and posterior teats characteristic of the female; *6*, the much closer teats characteristic of the male. (From Newman, after Lillie.)

differentiation of the individual is in a male direction. The change in sex trend takes place too late to result in the complete transformation of a prospective female into a typical male, for some female characteristics had already been fixed before blood admixture took place; but sometimes the transformation of sexes is nearly complete.

Nature furnishes a neat control experiment that strongly confirms the hormone theory of sex differentiation. Occasionally the fusion between the membranes of a male and of a female fetus is less extensive than usual, and as a result there is no anastomosis of blood vessels, and hence no crossing over of male blood into the female. As one might expect, there is no tendency for the female to be modified and both twins develop as normally as though they were singles.

Many other important hormones are known in man and in other animals, but those we have discussed are the best understood and the most important as regulators and coördinators of bodily processes. Their combined action aids immeasurably in the integration of the parts into a coherent whole.

D. Mechanisms of Nervous Coördination

Since we have already discussed in several places the morphology of the nervous systems of animals, it seems unnecessary to repeat here any general description of the gross anatomy of the nervous systems. Reference may be made concerning these facts to pages 403–405, where the nervous system of the frog is described and figured. The present section deals with the physiology of such a system.

The nervous system is, like every other system, composed of cells. The individual cells, or NEURONES (Fig. 225, **D**), have been described in some detail on pp. 419–421. Now the nervous system as a coördinating mechanism may be compared to a metropolitan telephone system with one main exchange, many minor exchanges and thousands of individual receiving and sending terminals. By means of such a system the complex community regulates many of its activities. In the organism the brain is the central exchange, while the spinal ganglia, sympathetic ganglia, and the sensory end organs represent the minor exchanges and receiving stations. The individual neurone is somewhat like the individual phone. The nerve fibers are like the telephone wires. Now there are special

receiving neurones (SENSORY NEURONES) and special sending neurones (MOTOR NEURONES). The sensory ones receive stimuli and transmit the message, while the motor neurones receive the message and relay it on to the various EFFECTORS, such as muscles and glands. In this way all parts of the body keep informed about

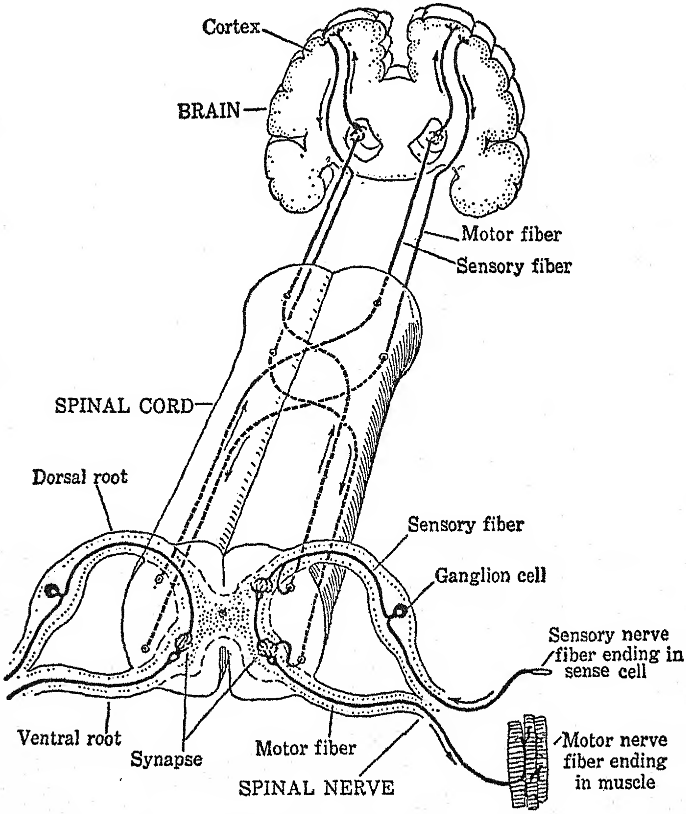


FIG. 231. Diagram showing the paths of sensory and motor nerve fibers. In the lower right part of the figure is shown a very simple case of a reflex arc. (From Woodruff.)

the rest of the body and the intricate complex of processes are coördinated and unified.

Reflexes.—The unit of effective nervous control is the *reflex arc*, which is carried out by the coöperation of sensory and motor neurones. In Chapter XXXIV we have already called attention to a number of specific reflexes in the frog. It is believed that the

whole behavior of the frog is at the reflex level. Reduced to its simplest terms, it may be said that a sensory neurone, on being stimulated sends its impulse over its axone to the spinal cord where, by means of its dendrites it forms a connection (SYNAPSE) with the dendrites of a neurone in the cord, which in turn passes the impulse to one or more other neurones in the cord. One of these neurones forms a synapse with the dendrites of a motor neurone and the message is sent along the motor fiber to a muscle or gland, causing it to react in whatever way its structure permits (Fig. 231). Such a piece of nervous behavior is termed a reflex. The response is automatic and may never arouse consciousness, though it sometimes does. In the reflexes discussed in connection with the processes of digestion consciousness is not usually aroused, but when the finger touches a hot object and is jerked away, the reflex operates promptly before consciousness of pain results. Now no reflex act involves a single reflex arc, for a stimulated area usually involves numerous sensory neurones and causes many muscle fibers or gland cells to react simultaneously. Theoretically, however, it should be possible for one reflex arc to come into action without affecting others. So, as we have said, we may regard the reflex arc as the fundamental unit of nervous activity. Higher types of nervous activity are believed to be derived from chains or complexes of reflex arcs.

The **conditioned reflex,** for example, is a new compound unit of a higher order induced by experience. The mouth-watering reflex of a dog, for example, may be induced without the smell, taste, or sight of food if, whenever the dog is fed a bell is rung as a feeding signal. Soon mouth watering occurs at the sound of the bell alone. Thus auditory neurones have been combined with the salivary reflex to form a new unit called a conditioned reflex. Learning is believed to consist largely of establishing more and more elaborate conditioned reflexes.

Instincts, in the strict sense of the term, may be defined as compound reflexes. True instincts, both the simpler and more complex, occur with machine-like regularity and are largely unmodifiable by experience. They are believed to depend upon fixed and inherited neurone patterns in the brain. A complex instinct is regarded as a "chain reflex," in which one reflex unit stimulates another, and this another, until the whole series is run off to the end. A good instance of this appears in the breeding be-

havior of birds. The birds mate, which sets off the nest-building reflex, which stimulates egg laying, incubation, feeding and care of young, etc. If one were to break the chain in the middle, say by removing the eggs from the nest, the whole series would have to be started over again, for the birds are unable to resume by simply laying more eggs.

Many of the more complex forms of behavior in lower and higher animals have been shown to be carried out through simple or complex mechanisms, and as such, are unconscious and machine-like. Thus a frog from which the cerebrum (its conscious center, if it has consciousness) has been removed swims about if placed in water. A pigeon without a cerebrum flies for a time after being thrown into the air, though it will not fly on its own initiative. Swimming and flying in these decerebrated animals are extremely complex, highly coördinated activities that have every appearance of being voluntary and purposeful, yet they have been shown to be no more than reflexes. Even in man, it is known through the study of his behavior under anesthesia, that many of his activities are carried on unconsciously and at the reflex or instinctive level.

While many reflexes of the simpler sort occur with such constancy and precision that the result of any given stimulus is predictable, there are many of the more complex sort of which this is not true. The more neurones involved in a complex nervous unit, the less predictable becomes the result of a particular stimulus. Thus some reflexes do not depend so much upon the character of the immediate stimulus as upon previous experiences and associations.

The important question now arises as to just how much of human behavior is reflex in the sense that any given act is determined by one's innate and conditioned reflexes: by his inherited nervous patterns, and by those established by previous experience. Some biologists consider every act thus predetermined, while others hold that much of a man's action is undetermined at any given moment, and that his action is the result of a free choice of alternatives. There is a real problem for you! Sorry we cannot offer you its solution.

In conclusion, it should be emphasized that the nervous system is *par excellence* THE coördinating and regulating mechanism, but it does not do this job all by itself. Numerous examples have been cited, and many more might be given, that show how the nervous,

hormonal, and gradient mechanisms collaborate in coördinating and integrating the processes going on in the organism. Together they constitute one exceedingly complex mechanism.

In speaking of reflex arcs we had occasion to mention sensory neurones as factors in the arc, but did not say anything about the organization of these neurones into complex organs, the sense organs. These will be discussed in the next chapter.

SUMMARY

1. The most important fact about organisms is that each is a unit in the sense that all parts are so integrated as to function together harmoniously.

2. The chief integrating mechanisms here dealt with are: physiological gradients, the system of hormones, and the nervous system. Other systems play a part in coördinating bodily functions. We need mention only the circulatory systems, the kidneys, and the mechanisms for temperature regulation.

3. In single cells and embryos the basis of organization is the existence of an axis, or axes, that are the visible expression of a gradient of physiological activity running from pole to pole. The apical pole of the axis has the highest rate of metabolism and usually acts as the center of organization. Integration in a life unit depends upon unified control just as it does in a business organization.

4. Various methods of demonstrating the existence of metabolic gradients in organic units are described, including susceptibility methods, decoloration methods, and direct measurements of oxygen consumption at different levels of the axis.

5. Endocrine glands are defined as glands that empty their secretions directly into the blood, in contrast with ectocrine glands that discharge their secretions through ducts to some region outside of the body proper: into the digestive tract or to the exterior.

6. The various glands of internal secretion (endocrine glands) constitute a system of coördinating and regulating mechanisms. The secretions of endocrine glands are called hormones and they act as catalysts of chemical processes going on in cells.

7. Thyroxin, the hormone of the thyroid gland regulates the rate of general metabolism. The activities of the thyroid are influenced by the hypophysis, another endocrine gland. The pancreatic hormone, insulin, regulates the consumption of blood sugar. The hormones of male and female gonads regulate the differentiation of secondary sex characters, and are in turn regulated by the hypophysis (pituitary gland).

8. The freemartin condition in cattle twins goes far to demonstrate the rôle of gonad hormones in the differentiation of the somatic structures of the two sexes.

9. The nervous system as a coördinating and integrating system may be compared to a metropolitan telephone system with a central exchange

and various regional exchanges, each of which has receiving and sending units with connecting lines between them.

10. The unit of effective nervous control is the reflex arc, which is roughly comparable to a combination of a sending unit of a telephone system, a switch board in an exchange, and a receiving unit.

11. Reflexes may be conditioned by experience so that new stimuli may become effective that were not so originally. Learning is a complex sort of conditioning of reflexes.

12. Instincts are regarded as complex associations of reflexes that are inherited and may be due to patterns of reflex arcs.

13. The question is raised but not answered as to whether all human behavior is the product of innate and conditioned reflexes.

CHAPTER XL

SENSE ORGANS

IN previous chapters we have referred to many sorts of sense organs present in the various types of animals studied. Very little attention, however, has been given to the physiology of these organs or to the ways in which the organism employs them to keep in touch with the environment. These matters are now to receive our attention.

Even among some of the more highly specialized Protozoa there are recognized certain specialized parts that serve as receptors of particular types of stimulation. As a rule, however, the Protozoa lack specialized receptors, the entire surface being sensitive to stimuli of all sorts.

In some of the lowest Metazoa, moreover, there is little or no specialization of localized sense organs. In Hydra, for example, the whole surface may be considered as a generalized receptor for a great variety of stimuli. When we come to Planaria, however, the eye-spots and the auricles constitute definite sense organs, the eye-spots being specialized for the reception of light stimuli and the auricles for mechanical and chemical stimuli.

A. SENSE ORGANS FOR CONTACT PERCEPTION AND DISTANCE PERCEPTION

Among the higher animals the organs of sense may be separated into two categories on the basis of whether they receive stimulation by direct contact with the object or whether they receive information about objects at a distance. Under the first type may be listed the tactile, temperature, olfactory, gustatory (taste), and equilibrium sense organs. Under the second type we may include only the auditory and the visual sense organs, although in a certain way the olfactory sense may also be thought of as a distance sense.

Among the contact senses we may characterize the TACTILE SENSE as that through which the organism becomes aware of the physical characteristics of surfaces. Closely allied with the tactile sense is the TEMPERATURE SENSE, for which there are special end-

organs distinct from tactile organs. The OLFACTORY and GUSTATORY sense organs are closely allied, the former receiving stimuli from chemicals in the gaseous condition, the latter from chemicals in the liquid state. The olfactory sense organs consist of specialized epithelial cells forming part of the lining of the nasal passages, while the organs of taste consist of little aggregations of specialized epithelial cells found in definite regions of the tongue and palate. In none of the types of sense units dealt with in the preceding paragraph is there any highly localized, compact grouping of the sensory elements into a well-defined organ. Those sensory units are merely specialized epithelial cells scattered over considerable surfaces. The situation, however, is far different in the remaining organs of special sense, those of equilibrium, of hearing, and of vision. Each of these deserves separate and special treatment.

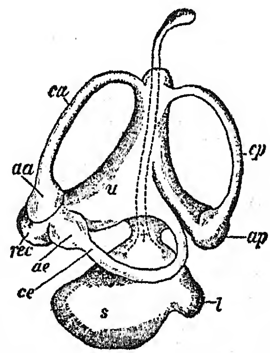


FIG. 232. Semidiagrammatic view of the left membranous labyrinth of a lower vertebrate. *s*, *l*, sacculus; *u*, *rec*, utriculus. The three semicircular canals are lettered *aa*, *ca*; *ae*, *ce*; and *ap*, *cp*. Laguna, *l*, a derivative of the sacculus becomes the cochlea of higher vertebrates. (From Wiedersheim.)

B. ORGANS OF EQUILIBRIUM

In the vertebrates, which we shall call upon to furnish examples of all the remaining types of sense organs, the organ of equilibrium consists of the SEMICIRCULAR CANALS. These canals form part of the MEMBRANOUS LABYRINTH of the inner ear, a complicated system of fluid-filled sacs and canals. The whole membranous labyrinth (Fig. 232) has two main parts, the SACCULUS and the UTRICULUS. From the utriculus come off the three semicircular canals, one in each major plane of space. The sacculus is mainly devoted to the reception of vibrations and hence constitutes the organ of hearing, about which we shall have a good deal more to say in the next section. For the present, let us confine our attention to the semicircular canals.

Each canal terminates in an enlarged bulb, or AMPULLA, at the point of communication with the utriculus. The epithelium of the ampullæ is especially sensitive to movements of the fluid in the canals which take place when the body changes its orientation

in space. The whole mechanism operates somewhat on the principle of a complex living spirit level that registers all changes in the orientation of the body. If the body tilts to the right, more fluid flows into the canal and ampulla inclined to that side. This produces an irritation in the nerve endings in that ampulla, an irritation that when conducted to the brain is interpreted as a definite tilt of the body in a given direction. Thus a bird flying, or a fish swimming in the dark, is able to keep right side up and trimmed both laterally and fore and aft.

Since the equilibrium sense necessitates immediate contact of moving fluid, it may be classed as a contact sense, but it differs from other contact senses in having a rather complex organ.

While in higher vertebrates the organ of equilibrium seems to be an accessory to the organ of hearing, this has not always been the case. On the contrary, there is good evidence that ancestrally the organ of equilibrium is older than the organ of hearing and that the membranous labyrinth was originally used mainly, if not exclusively, for equilibration. As evidence of this it may be said that in the lowest vertebrates now living, such as hagfishes and lampreys, the labyrinth seems to be almost entirely an organ of equilibrium, whereas the higher we go among the vertebrates the more important become the auditory specializations of this organ of dual functions.

C. Auditory Organs

The auditory organ of mammalian vertebrates is a complicated piece of machinery. In addition to the sense organ proper, which resides in the sacculus of the membranous labyrinth, there are several sound collecting and sound transmitting accessories. Referring to the illustration (Fig. 233), we see that the human ear consists of an OUTER EAR, consisting of a PINNA and an external auditory passage; a MIDDLE EAR, provided with an eardrum (TYMPANIC MEMBRANE) separating the outer and middle ears, a set of small articulated bonelets (MALLEUS, INCUS, and STAPES), and the EUSTACHIAN TUBE; and an INNER EAR consisting of the spirally coiled COCHLEA, a derivative of the sacculus.

The external ear functions as an ear trumpet for gathering and modulating sound waves; the middle ear is a sort of resonating chamber equipped with a vibrating membrane to which is attached a transmitting apparatus that conducts vibrations to the sensory

portion of the organ; and the inner ear contains the sound receptors. This whole mechanism is about as complex as a phonographic recording instrument and not unlike the latter mechanically.

The PINNA in man is quite degenerate as compared with those of some of the other mammals, notably the horse and other ungulates, in which we find a true sound-focusing trumpet. This instrument is provided with a set of muscles that turn it about in various positions in such a way that the direction of a sound can

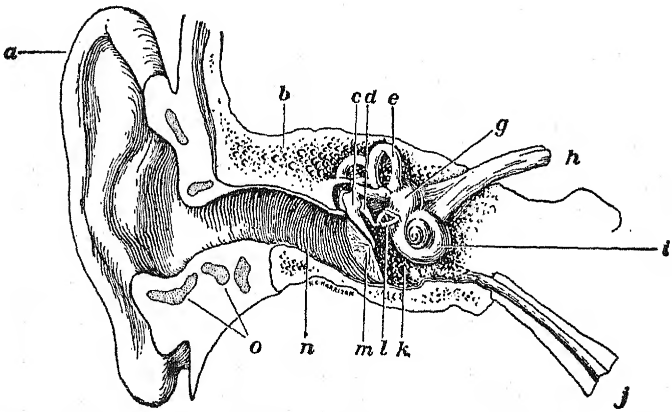


FIG. 233. Front view of the human organ of hearing, right side. *a*, pinna of outer ear; *b*, bone of skull; *c*, *d*, *l*, transmitting bones, malleus, incus, and stapes; *e*, one of the three semicircular canals; *g*, vestibule; *h*, auditory nerve; *i*, cochlea; *j*, Eustachian tube; *k*, tympanic chamber of middle ear; *m*, tympanic membrane; *n*, external auditory passage; *o*, cartilage. (From Woodruff.)

be determined. In man the same set of muscles is present in a paralyzed condition and the pinna is stiff and immovable, facts that indicate that the ancestors of man had movable ears.

The sensory portion of the auditory apparatus is located in the coiled COCHLEA. An examination of this structure shows the sensory epithelium in the form of elongated cells standing up more or less separately from the floor of the cavity. Each cell seems to terminate in minute bristlelike processes, that doubtless have to do with the reception of vibrations. In a sense, each sensory cell may be thought of as a living tuning fork capable of vibrating to sounds of a particular wave length. Each sense cell has a nerve fiber that runs to the auditory center of the brain, where

vibrations are translated into terms of sound. Over the groups of sensory cells there lies a membrane, known as the membrane of Corti, that is believed to act as a dampener for vibrations, thus preventing any more than a momentary vibration from one stimulus. This whole apparatus is known as the ORGAN OF CORTI, and is a fine example of a complex living mechanism.

D. ORGANS OF VISION

Of all the sense organs the eyes of the higher vertebrates are most readily interpreted in mechanistic terms, for they are con-

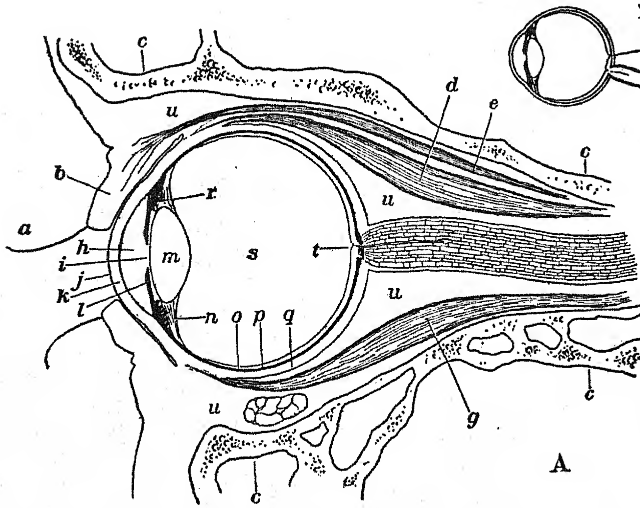


FIG. 234. A, vertical section of human eye *in situ*. B, horizontal section to show relation of optic nerve to fovea centralis (x), through which the optical axis passes. *a*, eyelash; *b*, lid; *c*, bony orbit; *d*, superior rectus muscle; *e*, muscle of upper lid; *g*, inferior rectus muscle; *h*, anterior chamber filled with aqueous humor; *i*, pupil; *j*, conjunctiva; *k*, cornea; *l*, iris; *m*, lens; *n*, suspensory ligament of lens; *o*, retina; *p*, choroid coat; *q*, schlerotic coat; *r*, muscles of suspensory ligament; *s*, vitreous chamber; *t*, point of entrance of optic nerve; *u*, fatty connective tissue. (From Woodruff.)

structed along lines analogous to those of man-made optical instruments, such as photographic cameras. The RETINA, though curved instead of lying flat like a film or plate, corresponds to the latter in being the light sensitive surface. The LENS of the eye plays the same rôle as the lens of the camera, at least up to a certain point. The IRIS of the eye operates in much the same way as

the diaphragm of the camera. The eyelids are like the shutter, and the eye socket like the case of the camera. Beyond this the resemblances cease and marked differences are to be noted. Thus the focusing mechanisms of the two instruments are utterly different: The camera is focused by sliding the lens back and forth, increasing or decreasing its distance from the plate or film; while in the eye the lens changes its shape through the action of muscles attached to its rim, thus focusing without changing the position of the lens. The illustration (Fig. 234) gives a good idea of the cameralike construction of the human eye.

The nervous components of the visual organ consist of the retina, the OPTIC NERVE, and the VISUAL CENTERS in the brain. Light rays of various wave lengths pass through the transparent chorion at the front of the eyeball, through the opening of the diaphragm-like iris (the pupil), and through the lens, by means of which they are focused on the retina in an inverted position. Each light sensitive cell (ROD or CONE) receives a stimulus from a ray of light of a particular wave length and transmits this stimulus along a nerve fibril to some cell in the visual center of the brain. There the various stimuli are correlated to form a mental picture of the object from which the light rays have emanated.

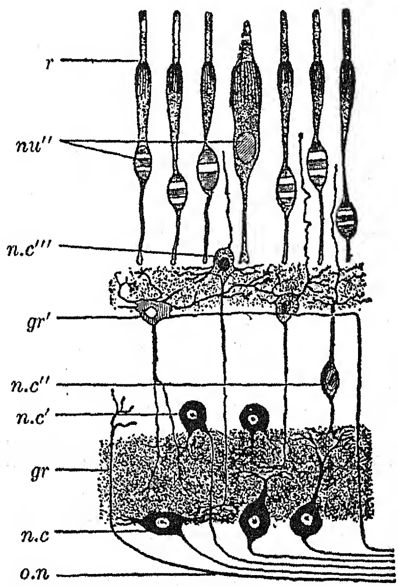


FIG. 235. Diagram of nervous elements of human retina. *gr*, *gr'*, granular layers; *n.c*, *n.c'*, *n.c''*, *n.c'''*, nerve cells; *nu''*, nuclear layer of rods and cones; *o.n*, fibers of optic nerve; *r*, sensory cells (rods and cones). (From Wiedersheim, after Stöhr.)

The RETINA consists of several layers, all of which are shown somewhat diagrammatically in Figure 235. The layer of nerve fibers lies next to the VITREOUS HUMOR of the eyeball. The layer of RODS AND CONES points toward the brain. The function of the other layers needs no special comment in a general discussion.

The eye as a whole is a very complex piece of machinery, which is to a very large extent self-operating and self-adjusting. Though imperfect in some respects, it is one of nature's finest mechanisms.

SUMMARY

1. Sense organs are here regarded as special mechanisms for adjusting the individual to its environment.
2. Sense organs may be broadly classified as organs of contact perception (tactile, temperature, olfactory, gustatory, and equilibrium) and of distance perception (auditory and visual).
3. The organ of equilibrium (semicircular canals) has a close connection with the organ of hearing. In the evolution of vertebrates the equilibrium function of the membranous labyrinth of the inner ear antedated the auditory function.
4. The auditory organs of man consist of the external pinna, the external auditory passage, the eardrum, the chain of bonelets (malleus, incus, and stapes), the Eustachian tube, and the spirally coiled cochlea.
5. All of the above, except the cochlea, may be considered as a complex apparatus for gathering and transmitting sound waves to the special receiving organ, the Organ of Corti in the cochlea.
6. The human eye as an example of a complex visual organ is compared to a camera with a photographic plate in position. The chief difference between eye and camera is in the method of focusing.
7. All parts of the eye except the retina are light transmitting and focusing structures. The retina is the receiving apparatus composed of light sensitive receptor cells, which receive stimuli and transmit impulses to the visual centers in the brain, where they are interpreted as visual images.

CHAPTER XLI

ADAPTATIONS IN GENERAL

A. Fitness in the Living World

"Adaptability," says ***Conklin,*** "may be defined as the power of self-regulation, self-preservation, and race perpetuation, by means of which living things are enabled not only to remain alive but also to adjust themselves to varied environmental conditions and to leave offspring. From the standpoint of any species the best that can happen is to increase and multiply, the worst is to become extinct. Self-preservation and race perpetuation are the *summum bonum;* everything that prevents or hinders these is injurious or unfit. Adaptability is a fundamental property of living things without which life itself could not long persist, for, as ***Herbert Spencer*** has said, life is 'the continuous adjustment of internal relations to external relations.' The origin of this or of any other fundamental property of life, such as metabolism, reproduction, or irritability, is shrouded in the same mystery as the origin of life itself."

It has long been the fashion among biologists as well as among the laity to marvel at the perfection of everything in nature. This is a backwash from the long prevalent doctrine of supernatural design, according to which everything was created perfect. Realization has gradually grown stronger and stronger that adaptiveness and fitness are purely relative terms. The most perfect adaptations we know leave much room for improvement. Even that wonderful adaptation, the human eye, falls far short of being a perfect mechanism. The well-known physicist, ***Helmholtz,*** is reported to have said of the human eye that, were an optician to send him so imperfect an instrument, he would send it back to him with the request that he learn his business. Yet in many respects the human eye is about as perfect an adaptation as there is in nature. Thousands of kinds of eyes, some of them many times less efficient than that of man, exist in successful types of organisms. Evidently, then, adaptation is a relative matter and there is room for improvement all along the line.

For many years after the publication of Darwin's *Origin of Species* the chief pursuit of naturalists seems to have been to seek out and to describe marvelous adaptations. So popular did this search after the wonderful in nature become that there arose a cult of "nature fakers," who, on the slenderest bases, built up extraordinary adaptive complexes that never existed and invented imaginary conditions to fit them. So uncritical as to adaptations was this period that it came to be assumed that everything about a surviving species must be adaptive, else it would have been eliminated in the course of natural selection. Thus, whenever apparently useless, negative, or even positively harmful characters were observed, these were explained as having at some former time been adaptive or as destined to have adaptive value in the future under changed conditions of life. Some even went so far as to assert that our failure to see the adaptive value of a character was due to our ignorance of its real function.

In spite of all this adaptation worship, it now has come to be generally admitted that many so-called adaptations have failed to meet a critical test of their values, and we are forced to conclude that every organism is a complex of both adaptive and nonadaptive characters. This being the case, it should be evident that nonadaptive as well as adaptive characters have evolved and that causal theories of evolution based entirely upon adaptive values of individual characters are in need of modification.

B. Suggested Explanations of Certain Types of Adaptations

a. Ontogenetic Adjustments.—Many phases of the general adaptiveness of organisms may be attributed to the molding effect of the environment upon the growing individual; for in order to grow up in any given environment an organism must be in harmony with the environment at every stage of development. According to this view there is no escape from fitness. Given a certain environment within which an organism must grow, the adaptiveness of an organism that succeeds in reaching maturity is inevitable. It is a common observation of experimental embryologists that any appreciable alteration of the environmental complex normal for a given species of embryo results in more or less profound modifications of the normal characters of the species. Such direct responses to changed environment are not truly adaptations,

except in the sense that living protoplasm is plastic and has the capacity to change under changed external conditions. What we call normal, then, may not be any more truly adaptive than the abnormal, but merely the particular structural expression that results when a certain kind of protoplasmic complex develops under the usual or prevailing environmental conditions.

Many other adaptations are at least partially due to functioning during development. In a fish embryo, for example, the heart musculature develops poorly and atrophies if, for any reason, the embryonic blood supply is cut off or seriously diminished. Again, in certain types of one-egg human twins it is not uncommon for the placental blood vessels of the two individuals to anastomose in such a way that one twin gets more than its share of the common blood supply. The result is that the blood pressure of one twin becomes seriously reduced, the heart has too little work to do, and either atrophies or becomes greatly reduced in size and in strength; while the heart of the other twin, with more than the normal amount of blood and thus more fluid to keep in circulation, becomes abnormally large and muscular. These and many similar facts that might be cited tend to show that much of the fitness of certain organs for special functions is the result of practice during embryonic periods and afterwards. Some writers go so far as to claim that all structure is the result of function, that function is merely a special form of chemical activity that leaves its mark as structure. Thus, function has been compared to a stream that molds its banks and bottom, leaves a sand bar here or makes an island there as structural evidence of its activity. While there is doubtless much truth in this point of view, it should not be forgotten that there are many organs of the most definite functional importance whose structure is complete before they have any chance to exercise their special functions. Thus, the human eye, which develops up to almost the definitive condition in total darkness, if it may be said to have functioned at all, certainly cannot have functioned as an organ of vision. Similarly, the lungs are almost fully formed before the infant gets its first breath of air; the organs of taste develop before there is anything to taste; and the vocal cords are well-developed before a single cry has been possible. It is obvious, of course, that all these organs have been functioning in a general way; they have had to carry on the ordinary processes of metabolism. But the point to be emphasized is this: that

they have not functioned in the particular ways that we call adaptive until the adaptive features have already reached their definitive condition.

b. Habitat Selection.—The claim has commonly been made by ecologists that much of the alleged fitness of organisms to their environment is due to the fact that many animals try out a great variety of environments and select the one best suited to their individual needs. When they find an environment best suited to them, they tend to stay there because all less suitable environments cause them more or less unrest. It is to be expected therefore, if the above thesis be granted, that any species that has locomotor powers and a wide range of environments to choose from will appear well-fitted to its environment. To what extent the theory of "habitat selection" solves the problem of the fitness of organisms to their special environments it is difficult to decide, but it is our conviction that only minor degrees of adaptiveness result from this factor.

Our purpose has been to present a fair and critical statement regarding fitness in the living world. While we are willing to grant that there has been a marked tendency to exaggerate the perfection of adaptations and to read into nature a universal fitness, we cannot agree with those who have attempted to explain away adaptations altogether by showing that they are all ontogenetic, i.e., repeated each successive generation under the molding influence of environment and function. This would be tantamount to a denial that any adaptations are hereditary. One extreme is as bad as the other.

C. Two Categories of Adaptations

There are, according to ***Conklin,*** two categories of adaptations: *a*, racial or inherited adaptations, and *b*, individual, acquired, or contingent adaptations. "Inherited adaptations are those which appear in the organism as if in anticipation of future needs and not as the result of present ones." In this category are the eyes, lungs, vocal organs, organs of taste, and many other organs of the human fetus. This is the kind of adaptation that the physiologist cannot explain away as merely due to the molding effect of environment or function or to habitat selection. Such adaptations have obviously evolved in some way, but there is as yet no really adequate theory as to the causes responsible for their origin and fitness.

D. Some Remarkable Inherited Adaptations

1. *The Bird an Adaptation for Flight*

One of the most thoroughly adapted organisms in the world is a flying bird. Its various flight adaptations seem to be as definitely built for their varied purposes as are the parts of an airplane; of the two, the bird does the job of flying more expertly than does the man-made machine. Both the bird and the airplane are to be classed as heavier-than-air flying machines. Now, the requisites for a heavier-than-air flying machine are somewhat as follows: *a*, broad planing surfaces capable of adjusting to varying wind pressures; *b*, minimum weight with maximum rigidity of framework; *c*, rapid and sustained production of power; *d*, steering

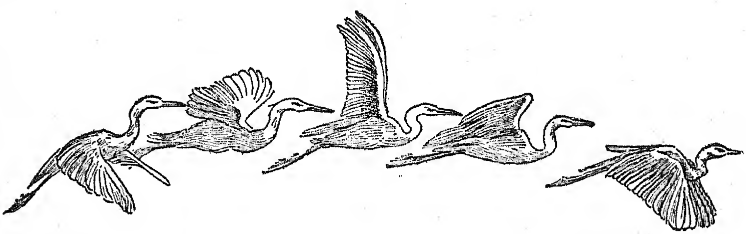


Fig. 236. Heron flying: showing clearly the mechanism of flight. (From Jordan and Kellogg, after Marey.)

and balancing devices. The bird meets the first requirement by means of its highly perfected flight feathers (Fig. 236), that co-operate in such a way as to make up a pair of planes with just the right amount of rigidity combined with enough flexibility to admit of the necessary adjustment to sudden or unequal changes of air pressure. The wings are also propellers; in this they are distinctly different from the planes of an airplane. The second feature of importance is that of economy of weight without sacrifice of strength and rigidity. The bird meets this condition by the use of well-known engineering principles, such as tubular instead of solid bones, the use of bony T beams, the use of diagonal braces and counterbraces of several kinds. Thus the bony framework of the bird has scarcely half the weight, as compared with the total body weight, of that in other vertebrates. Weight is further counterbalanced by the use of air sacs that fill all vacant spaces of the body, even the hollows of the bones, and by the use of feathers, whose lightness is proverbial, for planes, rudder, and body cover-

ing. Great and sustained power is secured partly through a most efficient engine—that great mass of pectoral muscles, whose work is nearly always so well within its capacity that tiring does not readily occur. Moreover, the lungs supply oxygen to the engine more effectively than do those of any other vertebrate; for the cold air goes directly to the air sacs, is heated before reaching the lung tissues proper, and then the exhausted air is passed out. There is thus a sort of through draft, and this prevents the admixture of pure with impure air. Even when at rest, the temperature of the bird's body is as high as 112 degrees Fahrenheit, and much higher when the bird is actively flying. At such temperatures metabolic activities go on more efficiently than at lower temperatures. For steering and balancing devices the bird has a tail capable of spreading fanwise so as to give a greater or less surface, and of lowering or elevating the path of flight. The planes, too, are jointed so as to enable them to adjust themselves to shifting wind pressures; while the head and the legs can be extended or drawn in to give the required balance. These and many other striking adaptations of the bird are examples of the kind of adaptations that are largely developed before they ever function in the particular ways for which they are adapted.

2. *Some Offensive and Defensive Devices*

Animals have anticipated man in the invention of nearly all of the standard methods of warfare. The use of armor has long been a favorite defense in such animals as the armadillos and the turtles. The use of spikes and spines of all sorts has been effective in such animals as sea urchins, hedgehogs, and porcupines. Attack-proof shelters have been made use of by mollusks, barnacles, trunkfishes, turtles, and armadillos.

The use of poisoned darts and spears has long been effective for both attack and defense in the cases of bees, wasps, scorpions; while many animals, such as serpents, lizards, spiders, and others, make equally effective use of poisonous fangs. As an expert in gas warfare let us recommend the skunk and his nonchalant tribe. The squid by shooting out his ink wad is said to becloud the water much as does a smoke screen in naval maneuvers. Killing by electric shock through charged wires is paralleled by several kinds of fishes (Fig. 237) in which masses of voluntary muscles have become modified in such a way that they function as storage batteries

of such efficiency that they are able to give off an electric discharge strong enough to stun a large enemy.

The art of CAMOUFLAGE was learned by man after a serious study of the various schemes for protective coloration in common use among animals. The scheme of blending with the background is the commonest of all color adaptations. Green insects fade from view among the green leaves or in the grass, and variously colored or mottled insects live among colored flowers or against the mottled background afforded by lichens. Kallima, the dead-leaf butterfly (Fig. 238), can scarcely be distinguished from a leaf. Transparent organisms live in the translucent waters of the sea. Many animals, such as chameleons and flounders, have the ability to change their colors in harmony with varied and changing backgrounds.

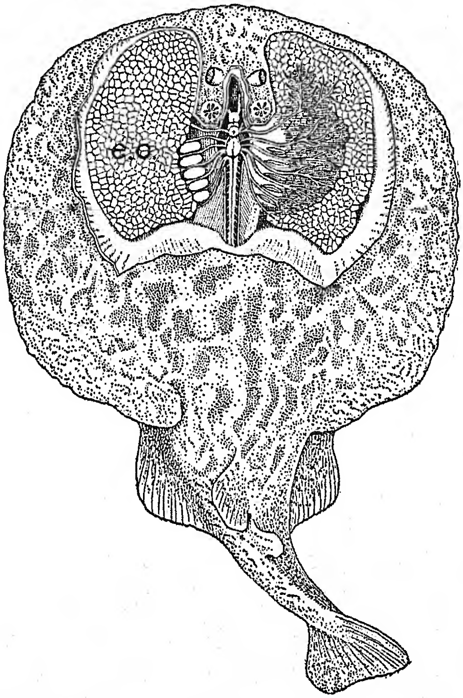


FIG. 237. The electric ray, showing the electric organs, e.o. (Redrawn after Leuckart-Nitsche wall chart.)

Many well-defended animals, such as wasps and venomous serpents, are commonly marked with contrasting bands or spots of different colors, a supposed adaptation said to function as a warning, like a sign reading "Dangerous. Keep off!" The idea involved is that birds or other enemies, once attacking these conspicuous animals and getting stung or bitten, will in the future associate an unpleasant experience with a particular color combination and avoid it. This furnishes the basis for another curious type of camouflage known as MIMICRY, the facts being these: Many otherwise defenseless animals resemble in very striking ways such animals as the bees and wasps, not only looking like them but

humming like them and behaving like them. The interpretation usually offered for this situation is that these mimics assume the colors of well-defended animals as a measure for self-defense, thus flying a false flag. In this place it would hardly be feasible to enter into a detailed discussion as to the validity of the supposed phenomenon of mimicry, but it should be said that some biologists are skeptical as to the reality of mimicry, and others strongly support it.

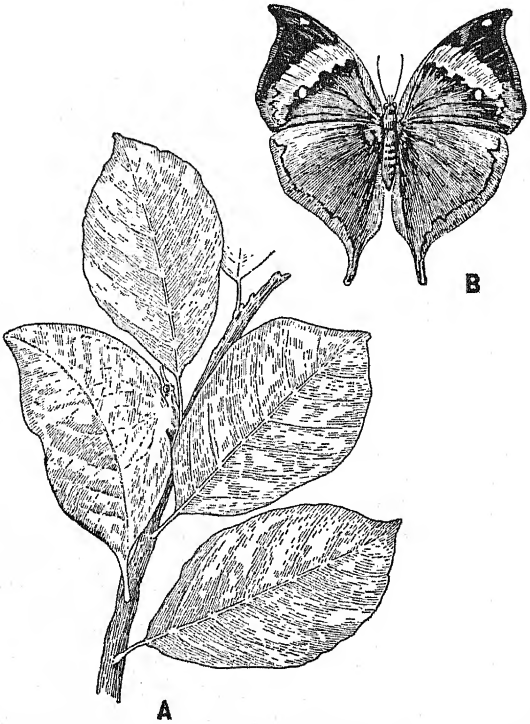


FIG. 238. *Kallima*, the "dead-leaf butterfly." A, butterfly resting among leaves; B, same seen from above with wings spread. (Redrawn after wall chart.)

The art of disguise has been highly perfected among animals. They very frequently make use of the scheme of looking like something harmless or attractive. Thus a well-known mantis, an insect of prey, looks almost exactly like a certain species of orchid blooms among which it awaits its prey. Nectar-hunting insects fly into the waiting arms of this living trap. In Java there lives a species of predacious spider closely resembling a bit of bird excrement upon which butterflies are wont to alight; and when they do so, they are caught and their blood sucked out by the disguised spider. The walking-stick insect (Fig. 239) exhibits as effective a disguise as any within our experience. In shape, in color, in rigidity, and immovability when in danger it perfectly simulates a twig. The same scheme is employed by many species of caterpillars (Fig. 240).

After all, however, there is no passive defense that compares in effectiveness with a good vigorous offense. Thus, the majority of animals, even those of peaceful dispositions who would avoid a fight by the use of concealment, when hard pressed make use of

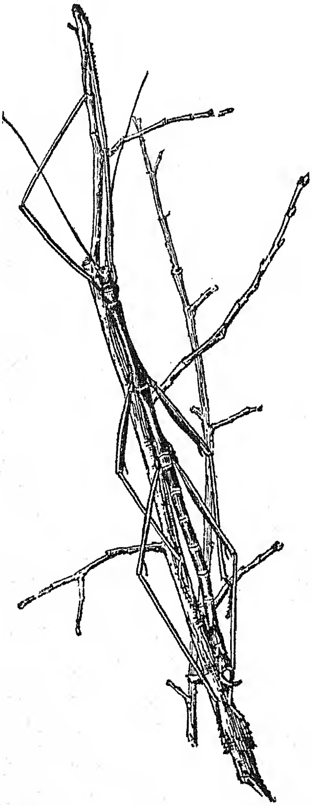


Fig. 239. A Walking-stick Insect, *Diapheromera femorata*, on a twig. (From Jordan and Kellogg.)

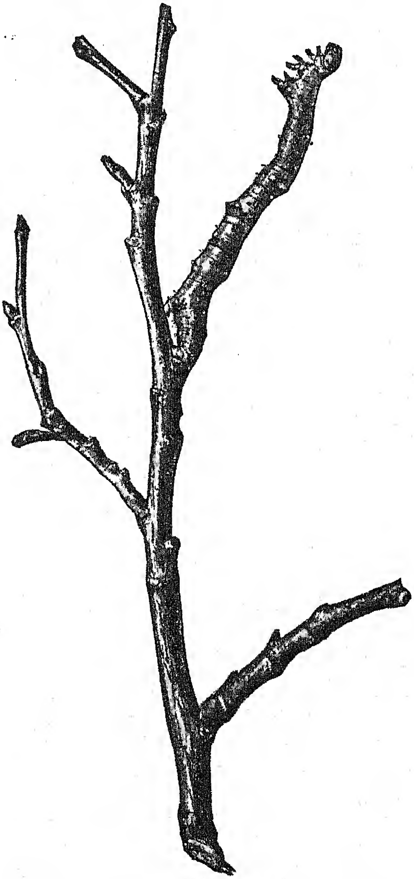


Fig. 240. Larva of a geometrid moth resting extended from a twig. (From Jordan and Kellogg.)

spurs, claws, teeth, fangs, horns, hoofs, spines, pincers, odoriferous glands, nauseous exudations, slimy secretions, and many other more or less offensive weapons, in a determined defense of life and liberty. All of the adaptations described in this section are inherited and are not ontogenetically molded by functioning.

3. *Adaptive Behavior*

Instincts of every degree of adaptive value exist among animals. Many animals, without any preliminary training at all, perform marvelously expert tasks. The building of elaborate nests by birds, by spiders, by fishes, are examples of the inborn equipment of animals. It is claimed by some authorities that a bird's first nest is rarely so good as subsequent nests, but even the first nest indicates the inheritance of a highly adaptive type of nervous response, already practically perfected as though in anticipation of its use. Likewise, the salmon, after spending five years in the sea, is impelled by an uncontrollable instinct to swim up the parent river to the headwaters where it had itself been spawned, there to mate and produce its progeny. In doing this the adult salmon wear themselves out through their long and strenuous exertions. This instinct is highly adaptive for the race, for it is essential that the eggs and young be laid in the cool, well-oxygenated waters of the headwater streams; but it is disastrous for a large percentage of the adult individuals.

The various instincts involving provision for and care of the young are among the most perfect of adaptations. The mother mud wasp builds clay galleries in which she stores fresh meat for the prospective young wasp grubs. The provender consists of living (sometimes dead) bodies of spiders or caterpillars, that have been stung in their nerve centers and thereby paralyzed. The instinct of the worker bees and ants to take care of and feed the young of the queen of the colony appears to be an instinct involving some evidences of altruism, but the authorities do not give it this interpretation. The workers are themselves females, but they are sterile and cannot have young of their own. Instead, they have an exaggerated obsession for taking care of the young of others, an instinct that is not infrequently imposed upon by parasitic dwellers in the homes of ants.

Instincts often appear precociously in larvæ in adaptation to an early need to shift for themselves. The most astonishing piece of instinctive behavior in very young animals was recently described by ***Hartman*** for fetal opossums. Seven days after the egg is fertilized the tiny opossum fetuses emerge from the maternal uterus as blind, naked, pink, grublike things less than a half inch in length. As they emerge one after the other, they quickly

turn toward the anterior end of the mother and begin to plow with surprising vigor through the dense hair of the mother's abdomen, using the abnormally large, flipperlike fore limbs with a hand-over-hand motion like that of a swimmer. Each little fellow plows its way through the hairy forest straight to the marsupial pouch of the mother, enters the latter, and finds a slender teat, which it swallows deep into its throat and holds fast by means of a precociously developed larval holdfast mouth. If more young are born at one time than there are teats—and this is usually the case—a struggle for the right to live ensues, and sometimes an early occupant is ousted from his claim by a stronger though later claimant. Once thoroughly clamped to a teat, the larva remains attached for weeks on end, and can hardly be pulled away from it. Hence, unless removed before it is fully established, its success is assured. Thus the standard of strength and aggressiveness is maintained through the elimination of the weaker offspring.

4. *Reproductive and Developmental Adaptations*

As has already been pointed out, the mitotic mechanism is ideally adapted to be the machine for the maintenance of the integrity of hereditary materials and for their transmission to progeny. Similarly, the mechanisms of maturation and fertilization are wonderfully effective adaptations for increasing variety in organisms and thus helping to furnish the raw materials for evolution. It has been shown that sex is an adaptation for increasing variability, and that all of the secondary sexual characters, including mating instincts and behaviors, are adaptations to facilitate the most important of all ends, racially speaking, that of increasing the numbers and therefore the dominance of the species; for in numbers there is strength and perpetuity.

Special breeding habits afford interesting examples of fitness. One common adaptation is that of carrying the young in the oviduct or uterus of the mother until it is sufficiently advanced to take care of itself. This phenomenon is known as VIVIPARITY and is in contrast with OVIPARITY, or the laying of eggs containing undeveloped or only partially developed embryos. Examples of viviparity range all the way from quite lowly organisms up to man, and it is found in some representative of nearly every large group. Thus, it is found in snails, in many insects, in spiders, in many fishes, in sharks, in salamanders, in snakes and in nearly all mam-

mals. In oviparous animals, where the young have to develop outside of the mother's body, many schemes for protecting the eggs are known, that of nest building being the most common. Some species make animated nests out of parts of their own bodies. Thus, the Surinam Toad (Fig. 241) lays her eggs, with the assistance of the male, upon her back; these sink into pits in the soft, spongy skin, where they remain until hatched out as competent young toads. Again, the sea horse (Fig. 242), a very curiously modified teleost fish, exhibits a kind of paternal care that would shame many a higher type. The father fish takes the fertilized eggs into his bosom, storing them in a brood pouch made by uniting his pelvic fins along their outer edges. He carries these about with him until they hatch, and even then does not abandon them but watches over them for some time.

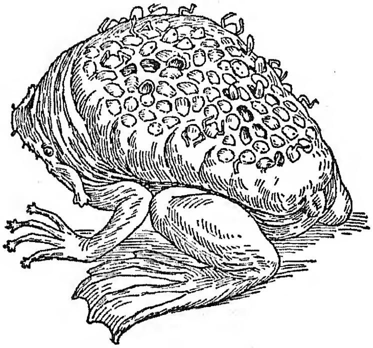


FIG. 241. The Surinam Toad, *Pipa americana*, showing method of rearing young on the back. (From Newman, after Lydekker.)

Examples of the solicitude of the mother for her young are so numerous as hardly to need comment, but are none the less important from the adaptational point of view. A lower animal can have no premonition of offspring, nor can she realize the relationship existing between herself and her young; yet she will frequently give up her life for her young. The instincts associated with reproduction are among the strongest and most unreasoning of all instincts, and the hardest to break up or change; witness the "setting" hen or the clasping male frog.

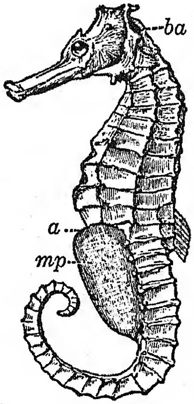


FIG. 242. *Hippocampus guttatulus*. Male, showing brood pouch (*mp*). *a*, anus; *ba*, branchial aperture. (From Boulenger.)

5. *Adaptations of Deep-Sea Animals*

One of the weirdest environments the world affords is the bottom of the sea at great depths. There it is dark and cold and almost lacking in oxygen, while the pressure is almost unbeliev-

ably great. Yet these vast and forbidding abysses are inhabited by all sorts of bizarre organisms. Fishes of many sorts (Fig. 243),

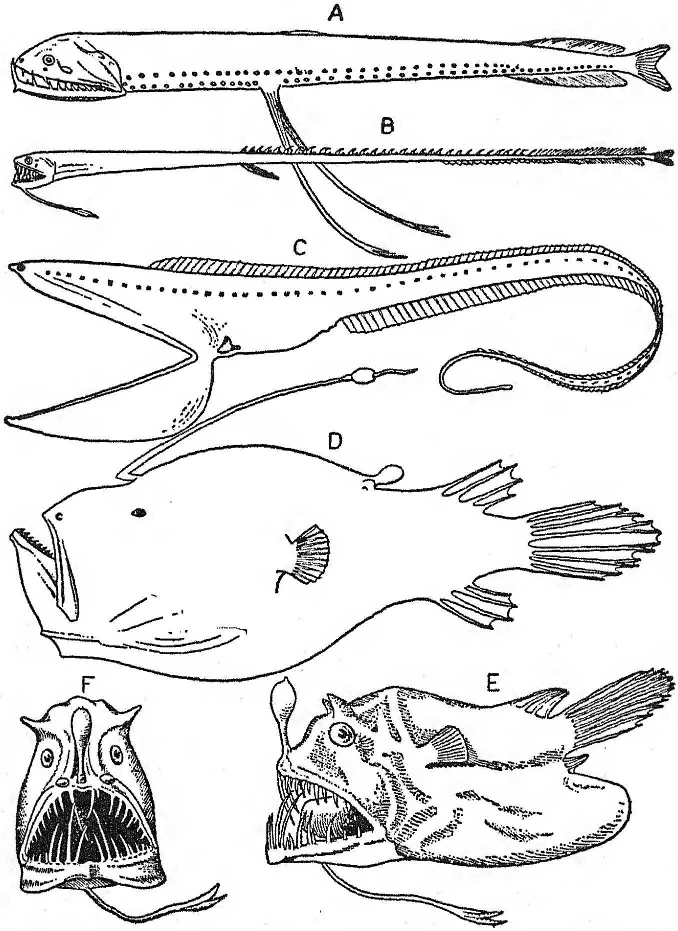


FIG. 243. Deep-sea fishes. A, *Photostomias guernei*, length 1.5 inches taken at 3500 feet; B, *Idiacanthus ferox*, 8 inches, 16,500 feet; C, *Gastrostomus bairdii*, 18 inches, 2300–8800 feet; D, *Cryptopsarus couesii*, 2.25 inches, 10,000 feet; E, F, *Linophryne lucifer*, 2 inches. (From Lull, after Goode and Bean.)

crabs, mollusks, worms, and many other forms thrive and multiply in this cheerless environment. We do not at all understand the nature of the adaptive mechanism that enables these animals to withstand the steel-crushing pressures that prevail at such depths

and that seem to bother them not at all. We do, however, know how some of the deficiencies of the environment are made good. Thus, many abysmal forms produce their own light by means of phosphorescent organs. Others have so-called telescopic eyes, which are highly effective in visioning lights of very low intensity. Could man view the sea bottom with the equipment possessed by these organisms he would doubtless add something very novel and weird to his scenic repertoire.

6. *Cave Animals*

Other creatures of darkness live curious lives in caves. Most cave dwellers are blind or nearly so, and usually have a pale, ghost-

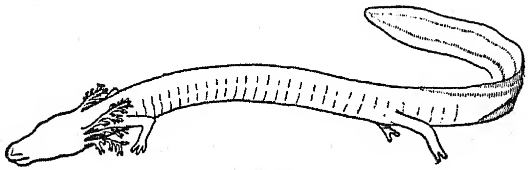


FIG. 244. Blind *Proteus anguinus*, from the underground waters of Carinthia, Carniola, and Dalmatia. (After Gadow.)

like appearance because of the lack of body pigmentation (Fig. 244). It goes without saying that such animals are better adapted to cave life than they would be anywhere else. One crying question in biology is: How did the cave animals become blind? In a later chapter an attempt is made to answer this question.

7. *Parasitism and Its Consequences*

The world is full of parasites, human and otherwise. The easy, sheltered life of the parasite is usually associated with a softening of fiber, physical and mental, and a consequent degeneration of those organs which serve a useful function only in an active, independent life. Thus, we find that extreme parasites lose their sense organs, their locomotor organs, and their active food-catching organs, and tend to degenerate into mere passive food-absorbing and reproducing machines. Some animals start out, as larvæ, to lead a free and independent life, but sooner or later lose their activity and become reduced to a sluggish, dependent condition. So dependent upon a specific host do some parasites become that they cannot live anywhere else. Some parasites are dependent

upon two or more hosts which they must inhabit successively during different phases of the life cycle; witness the flukes and the tapeworms already studied. The "nadir of parasitism" with the accompaniment of extreme degeneration is *Sacculina*, a description of which may be found on pp. 533–534 (see Fig. 262).

8. *Commensalism*

Many associations exist between different organisms in which the benefits are more nearly mutual than is the case in parasitism.

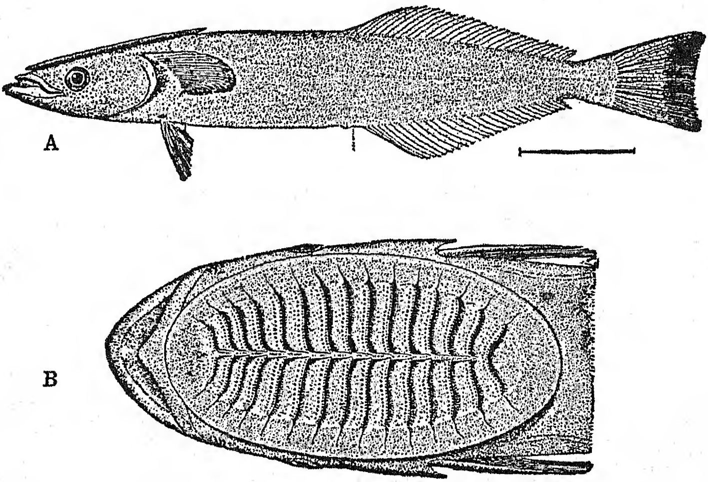


FIG. 245. A, the Shark Sucker, *Remora brachyptera*, Lowe; B, sucking disk of *Remora brachyptera*, Lowe, dorsal view. (From Jordan and Evermann.)

When no harm is done to either animal concerned in the commensal arrangement, but some benefit accrues to both, the condition is sometimes known as SYMBIOSIS. Some doubt exists, however, as to whether complete mutuality ever exists among commensals. A case in point is that of the shark sucker, Remora (Fig. 245), that attaches itself by means of a head sucker to the body of a shark and is carried about by the latter. Wherever the shark goes, the Remora gets free transportation and when he sees a convenient object of prey, he darts after it, devours it, and then returns to his accommodating conveyance. In this way the Remora, which is a good swimmer, conserves his strength for sudden, short forays after prey; but the relation lacks mutuality unless the

shark enjoys a sense of companionship. Various species of cœlenterates, such as jellyfishes and Siphonophora, harbor among their tentacles certain species of fishes. These tentacles are heavily armed with nematocysts, or nettle cells, which would readily be discharged by coming in contact with other species of fishes, but are neutral to the particular species that has been adopted as a commensal. The advantage of the well-armed shelter is obvious from the fishes' point of view, but wherein does the cœlenterate benefit? Figure 20 shows a species of Physalia capturing a fish, while Figure 246 shows another species of Physalia together with its commensal fishes apparently living harmoniously together.

Fig. 246. The Portuguese Man-of-War, Physalia, showing the various sorts of zoöids organized into an integrated colony. Certain elongated tentacle-like parts are used for paralyzing and capturing prey, but certain commensal fishes, as shown here, find shelter and protection from their enemies by swimming about among these tentacles, without themselves being in danger. Contrast this situation with that shown in Figure 20, where another species of Physalia is shown capturing a fish. (From Jordan and Kellogg.)

Some of the most remarkable instances of commensalism are found in connection with ant communities. In some cases two species of ants live together in the relation of masters and slaves. The master species is unable to perform even the simplest household duties, such as securing food, taking care of young, digging new galleries. In some instances they cannot even feed themselves unassisted and have to be fed by the slaves. The masters are specialists, doing only one thing well: they are fighters and marauders, with an instinct to raid the strongholds of the slave species and capture their young, which they take home for the adult slaves of their own household to rear. Here again mutuality is lacking, for

the slave species is quite capable of conducting its own life independently, while the master species is completely dependent upon the slaves.

9. *Societal Organization*

Many of the most successful species of insects owe their success largely to their tightly integrated social organization. Chief among these are bees, ants, wasps, and termites. Since the ants have

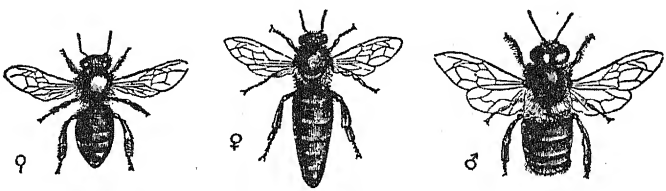


FIG. 247. The Honey bee, *Apis mellifica*, showing the three castes. (From Shipley and MacBride.)

already been dealt with in a previous chapter (Chapter XXVII), we shall confine ourselves for present purposes to a consideration of the special adaptations of the honey bee as illustrations of special adaptations for their peculiar mode of life.

Honey bees have been studied perhaps more extensively than any other insects largely because of their economic importance to man. They live in large communities of many thousands of individuals of which there are three castes: workers, drones, and a queen (Fig. 247). The QUEEN is typically the only functional female in the hive and is specialized for this function alone, lacking the specializations characteristic of the workers, which are sterile females. The queen has a life span of three or more years. She is larger, especially in the abdomen where eggs are formed, than are the workers. The DRONES are also larger than the workers and several of them are usually found in a hive. A drone is broad in the abdomen and his eyes are very large. He is a lazy creature, doing no work and living upon the bounty of the workers. His only function is to act as a mate for the queen, and hence he lacks specializations characteristic of workers.

The WORKER BEE is the caste about which we are chiefly concerned in this connection, for her adaptations (we use the feminine pronoun, although she is sterile) are so definitely correlated with

her work-a-day life. The worker may be regarded as, in a limited sense, an altruist, for she works for the good of the community, not for herself alone, and her adaptations are truly those favoring the survival of the species. In this place we shall confine our attention to but one group out of the many specializations involved in the complex life of the worker, namely, those for gathering pollen, the chief food of the colony.

The Legs of the Honey-Bee Worker, as Examples of Special Adaptations.—The legs of the bee (Fig. 248), like those of adult

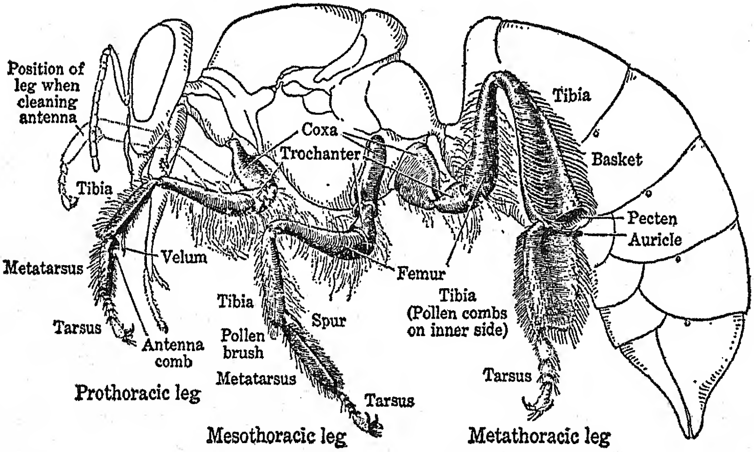


FIG. 248. Legs of the Honey bee. (From Woodruff.)

insects in general, are jointed structures with a definite number of differentiated segments. The five main parts are, beginning at the base: coxa, trochanter, femur, tibia, and tarsus. Some of the terms are taken over from names of parts of the vertebrate leg although there is no homology involved. The tarsus or foot is five-jointed, the terminal joint bearing claws.

There are three pairs of legs, each of which has a number of special functions besides walking. These legs are especially tools of the trade of pollen gathering, for pollen is the daily bread of bees, though they have other uses unconnected with this main function. Each leg and each part of each leg is minutely specialized for a particularized function. Let us consider the fore-, middle, and hind legs separately. The following description is taken largely from *Snodgrass*, who corrects some mistakes made in

earlier accounts. The forelegs are called prothoracic; the middle legs, mesothoracic; and the hind legs, metathoracic; but we shall use the common names for them.

The Forelegs.—These are the smallest of the three and the most mobile and active. Along the inner surface of the tibia occurs a fringe of short stiff bristles constituting the EYE BRUSH, used for cleaning pollen off the eyes. On a similar part of the tarsus is a longer row of bristles, the POLLEN BRUSH, used for scraping off pollen, picked up by contact, from the front part of the body. Near the base of the first tarsal segment is a very highly specialized tool, the antenna comb, a semicircular brush that fits the cylindrical antenna when the latter is drawn through it and cleans off the adhering pollen. A sort of spur (VELUM) projects down from the end of the tibia serving to hold the antenna snugly in position while it passes over the antenna brush. It will be seen that pollen handling is a messy job and, were it not for these special adaptations for keeping sense organs clean, the bee would quickly be blinded by sticky pollen and incapable of smelling and feeling.

The Middle Legs.—These are the least specialized and least mobile of the legs, having only a forward and backward movement. The large basal joint of the tarsus is covered with stiff hairs used for brushing pollen from the middle part of the body. Near the distal end of the tarsus is a long stiff spine used for picking out flakes of wax from the wax pockets on the under side of the abdomen. This instrument is of course not a pollen gathering adaptation, but aids in another important function, that of making the honeycomb.

The Hind Legs.—These legs are specialized for transporting pollen from flower to hive. The outer surface of the tarsus is smooth and concave and around its margin is a row of long incurved hairs, the whole forming the POLLEN BASKET, which is capable of carrying quite a large load of pollen. The basal joint of the tarsus (PLANTA) is very large and flattened, covered with sharp, stiff spines arranged in rows. It is a true brush, used for brushing up pollen from the body and from other legs and holding it until it is transferred to the basket. The distal end of the tibia is provided with a comb (PECTEN) which, acting in conjunction with another comb (AURICLE) on the proximal end of the tarsus, serves to rake off the pollen from the planta of the opposite leg and helps to store

it in the pollen basket of the opposite side. When the bee returns to the hive his two pollen baskets are usually loaded to overflowing. After reading this account of all these specializations for one of many life duties of worker bees one is forced to conclude that adaptations are very real and sometimes very exact and precise.

E. Individual, Acquired, or Contingent Adaptations

In contrast with inherited, or racial, adaptations, acquired adaptations arise in the individual during its lifetime under the stimulus of special environmental conditions, which may cause a marked structural or functional change or response in the somatic tissues. Examples of such individual adaptive responses are: the increased pigmentation of the skin in response to exposure to intense sunlight, the deposit of pigment acting as a light screen in preventing further injury to the cells of the skin; the increased thickness of the skin (callousing) as the result of friction which serves also to prevent injury; changed responses to higher or lower temperatures, which we call acclimation; the formation of antibodies in the blood when foreign toxic agents enter the body; regeneration of lost parts or healing of wounds; the increased strength or efficiency of organs resulting from increased use.

a. Sunburn.—It is well known that strong sunlight, especially those rays known as actinic, is injurious to living tissues, and that when a person exposes himself to the sun he gets sunburned. An incidental product of skin injury is the formation of brown pigment, which, if abundant enough, serves as a protection against further injury to the skin. So sunburn is an adaptive response, but is not inherited.

Many organisms respond to high temperatures and the accompanying drought by becoming more or less completely desiccated. Nevertheless when proper life conditions return, they take up water and resume their normal structure and activities. Other organisms can be gradually inured to high temperatures which, if applied suddenly, would kill or even cook them.

b. Tolerance to Poisons.—Tolerance to many sorts of poisons can be acquired if the initial dosage is small and the amount increased gradually enough. Thus is the drug habit built up, for the body adapts itself to the drug so that it requires larger and larger doses to produce the desired response.

c. **Immunity to Disease.**—Such immunity is but one of the adaptive responses of organisms to invasions of foreign substances harmful to the body. Certain diseases once recovered from cannot be reacquired, for the body has built up against the invading organism certain specific antibodies whose effect is to kill the invaders or weaken them to such an extent that the leucocytes can easily handle them. Thus, one who has had diphtheria cannot have it again because the body has elaborated in self defense certain permanent blood materials, antibodies, that inhibit the growth of diphtheria bacilli.

d. **Regeneration.**—The powers of organisms to regulate or regenerate lost parts or to produce whole individuals out of pieces is one of the most peculiar of the properties of living organisms, and, withal, one of the most strikingly adaptive of vital phenomena. In last analysis regeneration is merely a phase of reproduction, and we have already shown that reproduction is far and away the most important adaptation possessed by living things.

e. **Autotomy.**—Certain examples of the uses made of the ability of animals to regenerate lost parts are especially noteworthy in this connection. Taking advantage of their ability to regenerate lost organs, some animals have adopted the habit of self mutilation as an easy way of escaping an enemy. Thus a sea cucumber, when in danger of being eaten, eviscerates itself, shooting out its soft internal organs as a sop to the enemy, while the body wall escapes and is able to regenerate a new set of viscera. Similarly, a lizard, when seized by the tail by a pursuing enemy, gives up his tail by an apparently voluntary act, and easily regenerates another; while a crab, when seized by its claw by a more powerful adversary, breaks off its own claw and thus escapes a worse fate, the claw being only a temporary loss. These and similar instances of self mutilation throughout the animal kingdom illustrate the phenomenon of autotomy.

Conclusion.—While the above account of adaptations does not in any real sense cover the entire field of adaptive phenomena, it at least serves to indicate the nature of adaptations and how widespread is adaptiveness in organisms. Adaptations, in fact, are essentially part and parcel of life, and as such must be taken into account in any considerations dealing with the origin and development of organisms as we find them today. In listing the properties of living units we included among them adaptation as in-

dispensable for the maintenance of life. In this discussion of adaptations it has not been possible to deal exclusively with adaptations for self-preservation, for quite often these are curiously blended with adaptations for race preservation. We have reserved for special treatment, however, all those special mechanisms involved in reproduction proper as distinguished from those that are associated with the care of offspring.

The next chapter is to be considered as an extension of the present discussion of the relation of the organism to the environment, emphasizing a particular aspect of it.

SUMMARY

1. Opinions of zoölogists differ greatly as to the extent to which organisms are adapted to the environment. There are extreme adaptationists, moderate adaptationists, and adaptation skeptics.
2. A great deal of the special fitness of organs for functions and of organisms for particular niches of the environment may be due to ontogenetic adjustment or improvement by practise, on the one hand, or to habitat selection on the other.
3. There are, however, very numerous examples of inherited adaptations that are not due to ontogenetic adjustments. A number of typical inherited adaptations are presented as examples.
4. Instincts are discussed as adaptations.
5. Reproductive adaptations, especially those involved in the care of young, have mainly a racial value.
6. Among the most remarkable adaptations are those possessed by deep-sea animals.
7. Various kinds of animal associations that have adaptive values are discussed, including parasitism, commensalism, and societal organization.
8. A detailed study of the special adaptations of the honey bee for pollen gathering is given to illustrate how elaborately adaptive structure may be specialized to subserve a particular function.
9. A brief account of acquired adaptive responses is given, including sunburn, acquired immunity to disease, etc.

CHAPTER XLII

THE WEB OF LIFE

(A LESSON IN ECOLOGY)

One of the most skillful of modern biological writers, *Professor J. Arthur Thomson,* has written a chapter entitled *The Web of Life* in which he makes the following statement:—

"We may use the metaphor 'web of life' in two ways. On the one hand, Nature has woven a pattern which science seeks to read, each science following the threads of a particular color. There is a warp and woof in this web, which to the zoölogist usually appears as 'hunger' and 'love.' There is a changing pattern in the web, becoming more complex as ages pass; and *this is evolution.* But the essential idea of a web is that of interlinking and ramifying. We can never tell where a thread will lead to. If one be pulled out, many are loosened. This is true of Nature through and through.

"The phrase 'web of life' suggests another picture—the web of a spider—often an intricate system, with part delicately bound to part so that the whole system is made one. The quivering fly entangled in a corner betrays itself throughout the web; often it is felt rather than seen by the lurking spinner. So in the substantial fabric of the world part is bound to part. In wind and weather, or in the business of our life, we are daily made aware of results whose first conditions are very remote, and the chains of influence, not difficult to demonstrate, link man to beast and flower to insect. The more we know of our surroundings the more we realize that nature is a vast system of linkages, that isolation is impossible."

We must realize the interdependencies that exist within the organic world. Nothing can live unto itself alone. All species have numerous linkages with others. The following gem from *Thomson* will serve to illustrate the point:—

"**Nexus between Mud and Clear Thinking.**—To keep a famous inland fish pond from giving out, some boxes of mud and manure were placed at its sides. Bacteria—the minions of all putrefaction—worked in the mud and manure, making food for minute

Infusorians which multiply so rapidly that there may be a million from one in a week's time. A cataract of Infusorians overflowed from box to pond, and the waterfleas and other small fry gathered at the foot of the fall and multiplied exceedingly. Thus the fishes were fed, and, as fish-flesh is said to be good for the brain, we can trace a nexus between mud and clear thinking. What was the mud became part of the Infusorian, which became part of the Crustacean, which became part of the fish, which became part of the man. And it is thus that the world goes round."

Nutritive chains of this sort, reminding the author of *The House That Jack Built*, are very common in the world of life; in fact, there is probably no organism that does not form a link in one of these chains. ***Charles Darwin*** has given an account of one of these chains that is now famous:—

The Connection between Cats and Clover.—" Plants and animals, remote in the scale of nature, are bound together by a web of complex relations. . . . I have found, from experiments, that humble-bees are almost indispensable to the heart's-ease (*Viola tricolor*), for other bees do not visit this flower. I have also found that the visits of bees are necessary for the fertilization of some kinds of clover—thus 100 heads of red clover (*Trifolium pratense*) produced 27,000 seeds, but the same number of protected heads produced not a single seed. Humble-bees alone visit red clover, as other bees cannot reach the nectar. . . . Hence we may infer as highly probable that, if the whole genus of humble-bees became extinct or very rare in England, the heart's-ease and red clover would become very rare, or wholly disappear. . . . The number of humble-bees in any district depends in a great measure on the number of field-mice, which destroy their combs and nests; and ***Colonel Newman,*** who has long attended to the habits of humble-bees, believes that more than two-thirds of them are thus destroyed all over England." The relationship between cats and field mice is not far to seek, and is well stated by Colonel Newman: "Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice." Thus we see that the abundance of the clover crop in certain districts depends on the abundance of cats. A witty zoölogist has pointed out that, since spinsters tend to keep more cats than do other folk, the clover crop may trace back to the number of spinsters in a neighborhood.

The Relation between Fishes and the Pearl-Button Industry.—Some years ago the prosperous industry in pearl-button manufacturing along the Mississippi River was threatened with collapse on account of the pronounced falling off of the catches of clams. Alarmed at this situation, the Missouri state authorities commissioned ***Professors Lefever*** and ***Curtis*** of the State University to investigate the matter. It was found that the larvæ (glochidia) of the clam, after developing up to that stage in the gill chambers of the mother, sally out and gain attachment to the gills of certain fishes, a necessary step in their life cycle. After they have been freed from the gill cavity of the mother clam they float or swim about in the water until drawn into the gill chambers of certain species of fish. Contact with these tissues causes the bivalve glochidia to snap shut upon gill filaments, there to hold fast until the host tissue, under the stimulus of the adhering parasite, grows around the latter like a cyst or gall. Surrounded thus by highly vascular tissues, the young clams develop parasitically until they are ready to lead an independent life on the muddy bottom. The key discovery then was that the clams depend directly upon certain common river fishes, such as suckers, and that the depletion in the fishes had caused a corresponding depletion in the clams. The thing to do then was to build up the fish population by artificial propagation. This was done, and now, we understand, the button industry is thriving once more.

The Equilibrium of Nature.—One can scarcely realize how many elements enter into the nice balance of life in any complex community. Each organism in an ecological complex is definitely related to one or more other organisms, and the whole makes up an elastic web which cannot be broken in one place without raveling badly for some distance from the break and thus disturbing the balance of the whole. A typical example of a community in equilibrium is that in a fresh-water pond. The food relations in the pond are, according to ***Shelford,*** those shown in Figure 249. "Any marked fluctuation of conditions is sufficient to disturb the balance of an animal community. Let us assume that because of some unfavorable conditions in a pond during their breeding period the black bass decreased markedly. The pickerel, which devour young bass, must feed more exclusively upon insects. The decreased number of black bass would relieve the drain upon the crayfishes, which are eaten by the bass; crayfishes would accord-

ingly increase and prey more heavily upon the aquatic insects. The combined attack of pickerel and crayfishes would cause insects to decrease and the number of pickerel would fall away because of decreased food supply. Meanwhile the bullheads, which are general feeders and which devour aquatic insects, might feed more extensively upon mollusks because of the decrease of the former, but would probably decrease also because of the falling off of their main article of diet. We may thus reasonably assume that the black bass would recover its numbers because of the decreased

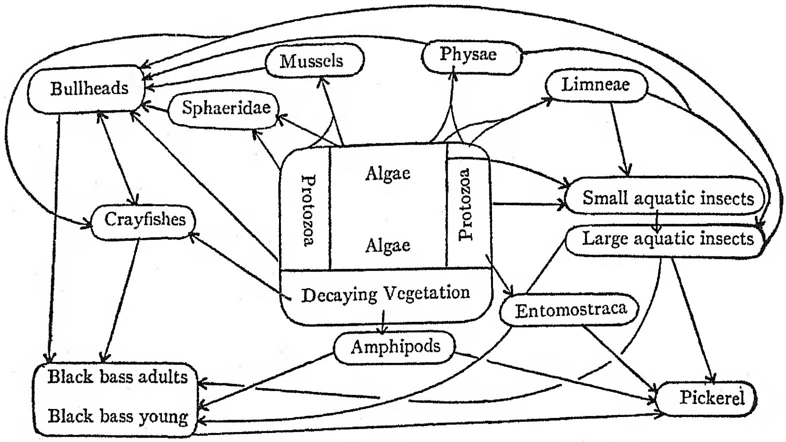


Fig. 249. Diagram showing food relations of a pond community. Arrows point from the organisms eaten to those doing the eating. (From Shelford.)

pickerel and bullheads, the enemies of its young." Shelford further points out that if, instead of merely diminishing in numbers, the black bass had been exterminated, an entirely new equilibrium would have to be established—an equilibrium that would probably involve the complete or nearly complete elimination of other elements in the complex.

Professor Forbes, a veteran student of animal life in the fresh waters, has pointed out the most important lesson that we must learn from a contemplation of the nice balance of nature: "There is a general consent that primeval nature, as in the uninhabited forest or the untilled plain, presents a settled harmony of interaction among organic groups which is in strong contrast with the many serious maladjustments of plants and animals found in

countries occupied by man. To man, as to nature at large, the question of adjustment is of vast importance, since the eminently destructive species are the widely oscillating ones. The insects which are well adjusted to their environments, organic and inorganic, are either harmless or inflict but moderate injury (our ordinary crickets and grasshoppers are examples); while those that are imperfectly adjusted, whose numbers are, therefore, subject to wide fluctuations, like the Colorado grasshopper, the chinch bug, and the army worm, are enemies which we have reason to dread. Man should then especially address his efforts first, to prevent any unnecessary disturbance of the settled life of his region which will convert relatively stationary species into widely oscillating ones; second, to destroy or render stationary, all the oscillating species injurious to him; or, failing in this, to restrict their oscillations within the narrowest limits possible. For example, remembering that every species oscillates to some extent and is held to relatively constant numbers by the joint action of several restraining forces, we see that the removal or weakening of any check or barrier is sufficient to widen and intensify this dangerous oscillation, and may even convert a perfectly harmless species into a frightful pest."

The lesson here pointed out is obvious. Man should beware of senseless slaughter even of animals that appear to him to be useless or even a nuisance, lest a worse thing befall him. The killing of snakes is to be decried: they occupy a position in the web of nature where many strands cross and thus play a useful rôle in maintaining a stationary balance. The deforestation of large areas has had a very bad effect not only in lessening the rainfall but in removing animals that prey upon agricultural pests. The question arises as to whether any animal is valueless. It is easy to assume that the extermination of some forms of animal life could be only a boon to mankind; but it is difficult to be sure that the results would all be so beneficial as we might assume. What, for example, would become of the parasites that now pass part of their life cycles in these despised animals? It is not inconceivable that these parasites might be forced to invade and adapt themselves to the bodies of man's domesticated animals or even to the bodies of men themselves. Parasites that are fairly benign in the bodies of lower animals sometimes cause the most virulent diseases in man and his stock animals. This then is a question worth pondering over.

Charles Darwin was the first man to make clear the fact of nature's intricate interconnections. It was the realization of what we have been calling the *Web of Life* that led him to value even small changes in species and to believe that no change that might take place in a balanced system could be considered as unimportant. Adaptations, he thought, must be considered not as isolated phenomena, but each one in relation to the whole intricate system of interdependent species.

SUMMARY

1. The *Web of Life* conception is presented in order to emphasize the fact that life units in nature are not isolated entities, but are linked together by a vast system of mutual interdependencies.
2. Examples of intricate interdependencies are given, including the "nexus between mud and clear thinking," the connection between cats and clover, etc.
3. Cases of the equilibrium of species in an ecological complex are given, such a complex as a pond community constituting one of the more complex life units, integrated by a system of interdependencies.
4. In dealing with problems of organic evolution it is necessary to have in mind the *Web of Life*. No species evolves alone, but groups of species adjusted to each other evolve together.
5. This chapter deals with some of the aspects of that branch of Zoölogy known as Ecology.

PART VI

MECHANISMS OF RACIAL MAINTENANCE AND ADJUSTMENT

(EVOLUTION AND GENETICS)

CHAPTER XLIII

REPRODUCTIVE MECHANISMS

In this chapter we propose to classify and discuss all of the principal modes of reproduction in the animal kingdom. These various methods of maintaining the continuity and perpetuity of races and species are to be thought of as only one part of the adaptive mechanism of race preservation. In the chapter on *Adaptations* various structural and behavioral mechanisms for the care of eggs and young have already been dealt with. In this chapter we shall confine ourselves to a discussion of the various methods by means of which the bodies of parents give rise to offspring.

A. Two Main Kinds of Reproduction

Several schemes for classifying the various modes of reproduction have been offered. For a long time the standard categories of reproduction have been spoken of as sexual and asexual, but this has certain unsatisfactory features. In the recently revised edition of his book, *The Cell*, ***Wilson*** suggests the two categories SOMATOGENIC and CYTOGENIC, "the former including asexual multiplication by fission or budding in which the body itself divides to produce offspring that are essentially multicellular fragments of itself. Cytogenic reproduction (cytogony) on the other hand, is effected by means of unicellular GERM CELLS which by growth and division may build up a new multicellular body. In the Protista this distinction does not properly exist, since the whole body is in itself unicellular; here also, nevertheless, it is convenient to speak of reproduction as cytogenic."

According to this view somatogenic reproduction must be always asexual, for no sex act is involved; but cytogenic reproduction may be either sexual or asexual. Thus reproduction by spores may be classed as cytogenic, for a whole new individual arises from a single cell. In the majority of animals cytogenic reproduction involves the union of two germ cells, GAMETES, to form a ZYGOTE, but there are very many in which the egg, female gamete, is able to develop without union with the male gamete, a process known as PARTHE-

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NOGENESIS. This process is not to be thought of as a type of spore reproduction but as a secondary modification of SYNGAMY, or reproduction by the union of gametes.

The various modes of reproduction will now be discussed without attempting to separate completely the cytogenic and somatogenic modes.

B. Modes of Reproduction Described and Discussed

1. *Transverse Fission*

We have already encountered, in dealing with the various types of animals presented in Part II of this text, several specific instances of transverse fission—namely, in Paramecium (Fig. 98), in Planaria (Fig. 129), in the tapeworm (Fig. 135). In all these cases it is thought that, either because of the elongation of the principal axis or a slowing down of the metabolic rate of the apical or controlling region—probably for both of these reasons—the basal or posterior part of the organism gets out of control and ceases to be an integral part of the parent organism. At first it becomes independent physiologically without showing any visible morphological evidences of isolation; but later, actual physical separation takes place and a new apical region appears, a definite indication that a new individual has been produced.

2. *Lateral Budding*

An excellent example of lateral budding is that described for Hydra (Fig. 115) and for the colonial cœlenterates, such as Bougainvillea (Fig. 123). This type of budding is more plant-like than animal-like, and is characteristic of forms that are fastened to the substratum by the basal end so that they are not free to cut off the posterior part without casting adrift the anterior part. When a new individual arises, it does so at a point far distant from the apical end, where the dominance of the apical end has become weak. A lateral outgrowth occurs with a new axis of its own approximately at right angles to the parent axis. The rapidly growing tip of the bud becomes the new apical region, and this proceeds to organize the outgrowth into a new individual that may or may not break loose from the parental body. In Hydra the buds always break off and become free; while in the colonial hydroids only certain highly specialized buds, medusa buds, break loose, and these become independent sexually mature individuals.

Among the higher phyla of animals lateral budding is found only in association with degenerate bodily conditions and sessile life. Among the chordates, for example, lateral budding is common in the colonial TUNICATES, or sea squirts. By this method of reproduction elaborate colonies are formed, as in Pyrosoma (Fig. 250), where the individuals are so arranged as to give the colony

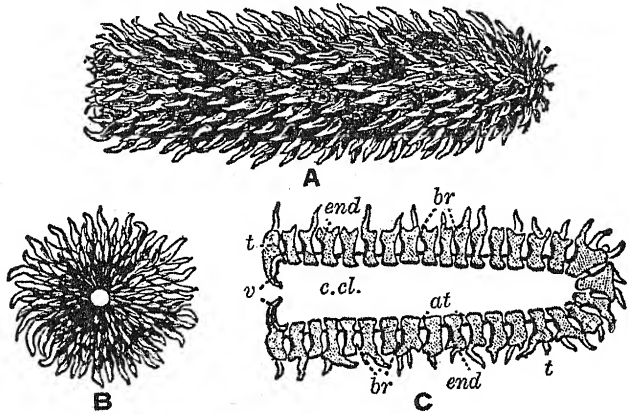


FIG. 250. The free-swimming colonial ascidian, *Pyrosoma.* A, lateral view (nat. size); B, view of the open end; C, diagram of longitudinal section; *at*, atrial pores opening into the central cavity or cloaca, *c.cl*, of the colony; *br*, branchial or oral apertures opening to the outside; *end*, endostyle; *t*, test or tunic; *v*, velum or diaphragm at terminal opening. (From Herdman.)

the appearance and the action of a single individual of a higher order; for the numerous zoöids behave as though under one centralized control.

3. *Longitudinal Fission*

We have shown that, in transverse fission, the original anterior or apical end remains the same while a new basal individual, at first subordinate to the apical individual, is cut off. Thus the products of transverse fission are characteristically unequal at the time when the division occurs. The same is true of lateral budding. In longitudinal fission, however, two equivalent individuals are produced from two equal halves of the parent individual. The daughter individuals are true twins and are essentially alike in all respects except that one is the mirror image of the other. Moreover, neither individual is subordinate to the other.

This kind of reproduction is common in the Protozoa, especially

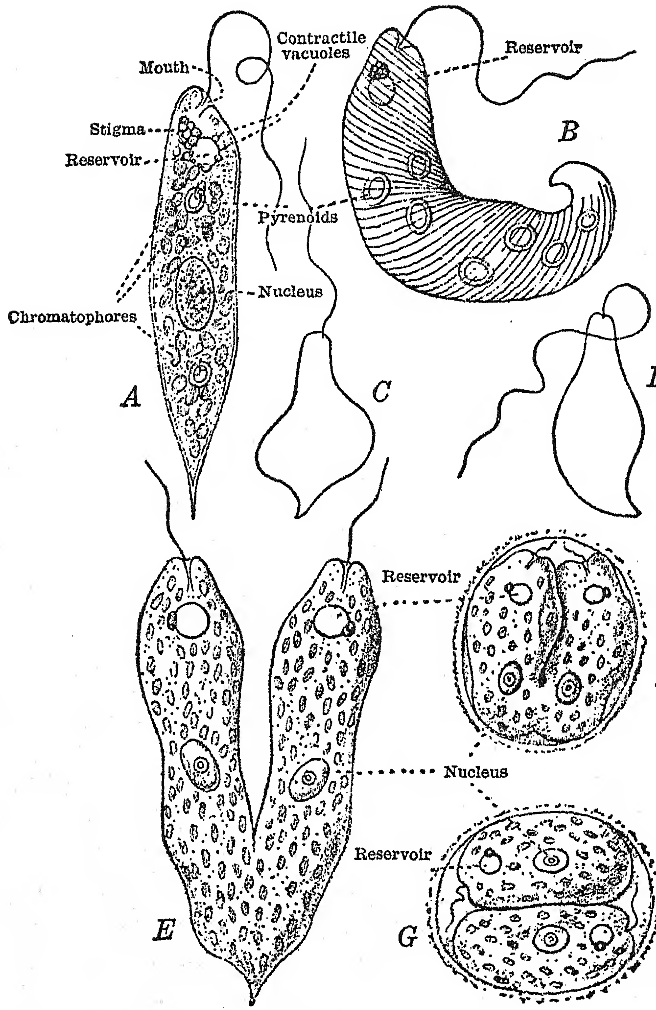


FIG. 251. *Euglena viridis*. *A*, view of free-swimming specimen showing details of structure; *B*, another animal showing change of shape and striations; *C* and *D*, outlines showing stages of contraction; *E*, reproduction by longitudinal fission; *F* and *G*, division within a cyst. (*A–D*, from Bourne; *E–G*, from Bourne, after Stein.)

in the CLASS MASTIGOPHORA. The fission of Euglena (Fig. 251) is typical. Here the nucleus divides after elongating transversely, and the cytoplasm follows suit, splitting first at the anterior and last at the posterior end. The two individuals, as they lie before separation, are seen to be mirror-image duplicates of each other, a characteristic feature of true twins. Among the higher organisms TWINNING is of quite frequent occurrence. Even in man we have DUPLICATE TWINS which often show mirror-image symmetry between the two individuals; and there is strong evidence that such twins are the products of the longitudinal fission of the early embryo. In the nine-banded armadillo (Fig. 252) twinning of this sort is a specific characteristic. In practically every litter there are four young, all of a litter being of the same sex. It is now definitely known that in this species the early embryo divides by fission to form twin embryos, and that almost at once each twin divides again by longitudinal fission, thus giving rise to two pairs of duplicate twins—QUADRUPLETS, as they are commonly called. Such quadruplets are much more nearly identical than are brothers or sisters derived from different germ cells of the same parents. The four individuals derived from one fertilized egg inherit but one assortment of hereditary genes, while ordinary brothers or sisters inherit each a different assortment. Partial twinning gives rise to Siamese twins and a long array of two-headed monsters, or forms with one head and two bodies. Twinning is common in earthworms, in echinoderm larvæ, in Amphioxus, in fishes, in frogs, and in many other animals. The conditions that favor twinning are to a certain extent known. It appears that any agency that lowers the rate of development at a critical period, when the axis of symmetry is being established, may induce the partial or complete isolation of the primordia of the right and left halves of the axis, and cause each lateral half to behave like an independent individual. Here again the basis of reproduction is PHYSIOLOGICAL ISOLATION, followed by physical separation of parts of an individual and the regeneration of a whole individual from a part.

4. *Internal Budding*

We have not yet encountered a case of internal budding. It occurs chiefly among Porifera (sponges) and Bryozoa (moss animalcules), two relatively low phyla. The characteristic feature of this type of reproduction is that minute representative aggre-

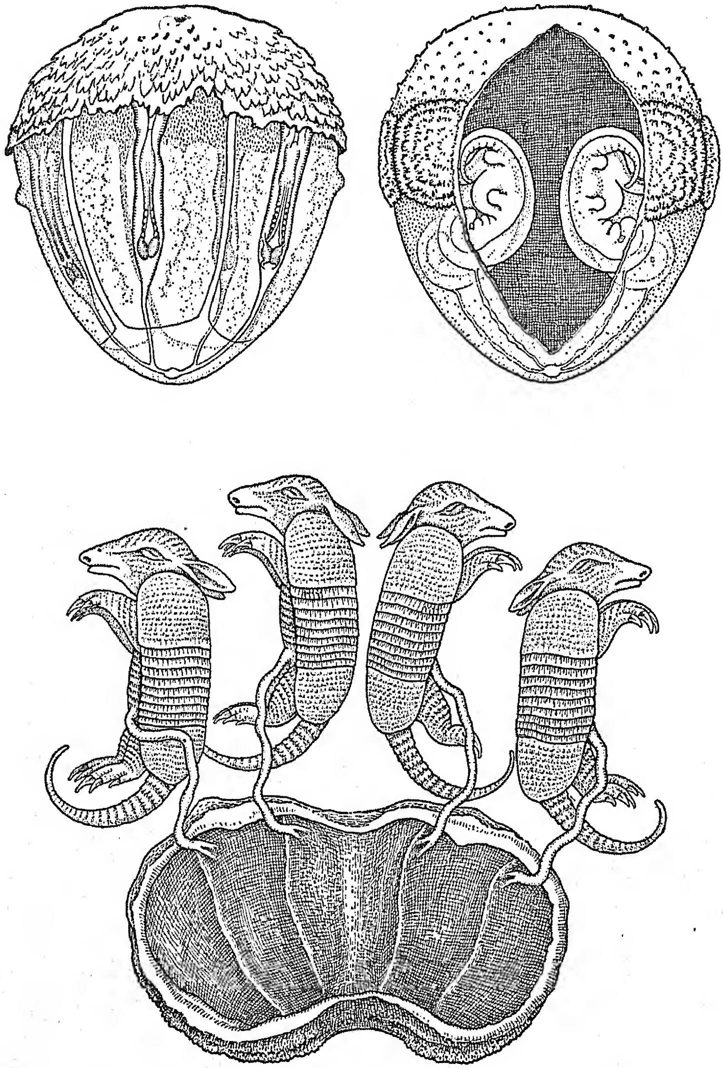


FIG. 252. Three stages in the development of armadillo quadruplets. In each case the four individuals have been obtained by the fission of a single embryonic primordium. In the lower figure the egg has been cut open and the fetuses removed, but left attached to the egg membranes by means of their umbilical cords. (Original.)

gations of cells are cut off from various internal parts of the parent, without any direct reference to the axes of the parent. These little sample packages of cells are known as GEMMULES (Fig. 253) in the sponges, and STATOBLASTS in the Bryozoa. In gemmule formation, a small mass of representative cells, consisting of samples of each of the kinds of cells in the parent body, proliferate in the loose MESOGLŒA, the gelatinous middle layer of the sponge. The cell mass rounds up and becomes inclosed in a dense coat of spicules. In this state the young gemmule is capable of surviving the death of the parent and of developing a new sponge when the parent body breaks up. Gemmules float about far and wide in the sea currents, and the species is thus distributed over large areas. In most of the points mentioned statoblasts are essentially similar to gemmules.

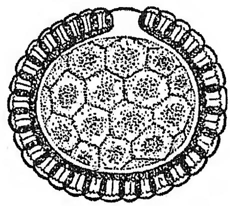


FIG. 253. *Spongilla.* A single gemmule, seen in section, showing the thick wall with its opening, and the central mass of germinal cells. (From Weysse, after a Leuckart-Nitsche wall chart.)

5. *Sporulation*

A great many species of Protozoa, not only within the Class Sporozoa but in other groups as well, reproduce by spores. The process of sporulation is one involving repeated nuclear divisions, at first not accompanied by divisions of the cytoplasm but sooner or later resulting in the formation of a large number of excessively minute nucleated masses of protoplasm, sometimes naked and sometimes in elaborate capsules. These minute cells are spores and the process is called sporulation. Each spore is of course a sort of minute "germ cell"; for each is capable of reproducing a new individual of the species. A good example of sporulation is that of the protozoan parasite, *Coccidium schubergi*, which is found in the intestine of the centipede, *Lithobius forficatus.* The life cycle of this form is shown in the accompanying illustration (Fig. 254), where the events in the history are numbered from I to XX. Part of the life cycle takes place in the body of the centipede and part of it outside. The centipede, in feeding, picks up cysts of the parasite such as that shown in XX; from these cysts minute sporozoites (I) emerge and enter the cells of the intestinal wall (II), where they multiply (III, IV) and form numerous small cells (V, VI, VII) that in turn become motile individuals (VIII, IX, X). These free

motile individuals, merozoites, which are really spores, then proceed to differentiate into sex cells, some growing large and becoming female gametes (XI *a*, *b*, *c*), others multiplying more rapidly and remaining small male gametes (XII *a*, *b*, *c*, *d*, *e*). Male gametes unite with female gametes to form the equivalent of zygotes

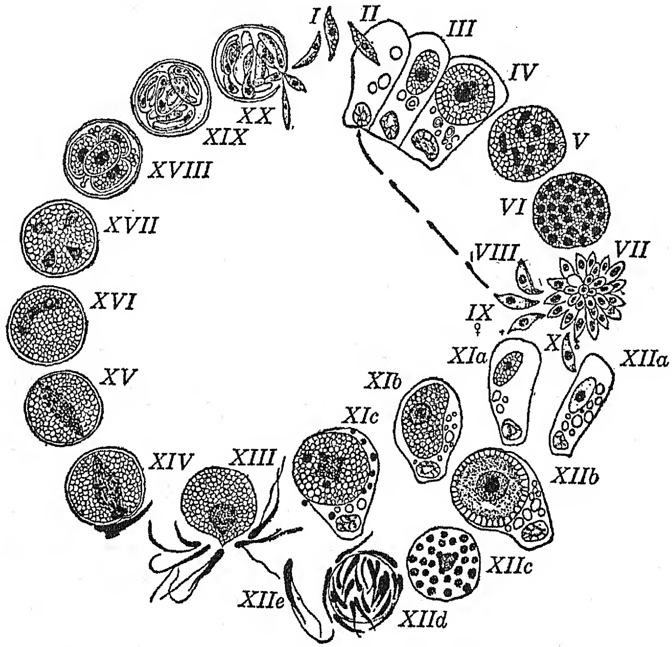


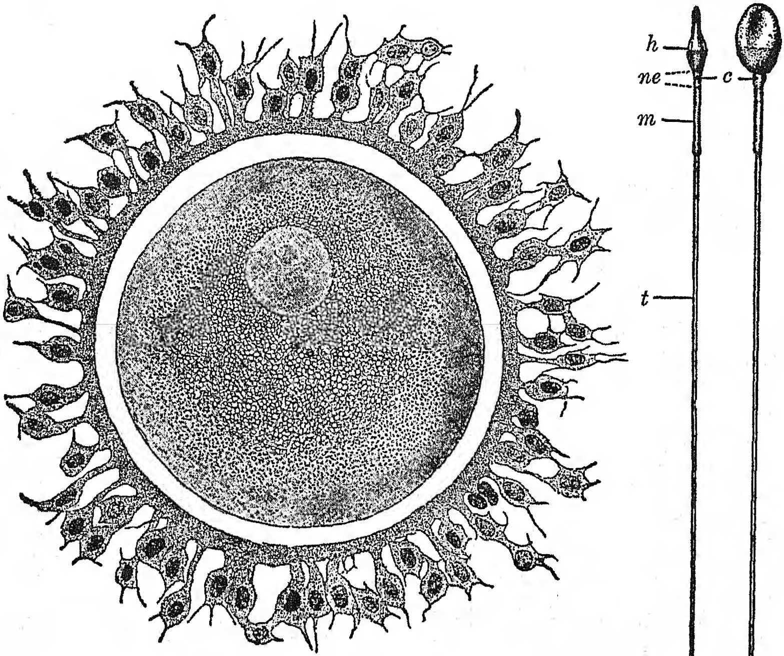
FIG. 254. Reproduction in the protozoan parasite, *Coccidium schubergi*. *I*, sporozoites. Stages represented by stages *II–VII* and *XIa–XIIc* are intracellular; *IV–VIII*, represent sporulation; *IX–XIII*, developing gametes; *XIV–XX*, development of spores. (From Shull et al., courtesy of McGraw-Hill Book Co.)

(XIII, XIV, XV) and something like cleavage takes place (XVI–XX), resulting finally in the production of numerous asexual sporozoites like those we started out with. Thus in the life history of a parasitic protozoan we see two modes of cytogenic reproduction, the one asexual (by means of spores), the other sexual (by means of gametes).

6. *Gametic Reproduction*

Typical gametic reproduction involves, as the name implies, the union of two gametes to form a combination cell or zygote. In

the metazoa there are two kinds of gametes, ova and spermatozoa (Fig. 255), which unite to form the zygote or fertilized egg. In the higher forms the gametes are the only cells that have retained the capacity to produce new individuals. A highly characteristic feature of gametes is that they undergo maturation divisions. If,



A

B

FIG. 255. Human egg cell, ×415, and sperm cell, ×2000. A, Egg just removed from the ovary, surrounded by follicle cells of the ovary and a clear membrane. The central part of the egg contains metaplasmic bodies and the large nucleus. Superficially there is a clear ectoplasmic region. (After Waldeyer.) B, two views of the human sperm. *c*, centrosome; *h*, "head" consisting of the nucleus surrounded by a cytoplasmic envelope; *m*, *ne*, middle piece; *t*, tail or flatellum. (From Woodruff, after Retzius.)

as sometimes happens, an individual arises from a single cell of an early embryo, as, for example, a blastomere of a cleavage stage, this is not a case of gametic reproduction, for such a cell does not undergo maturation. Another point that should not be forgotten is that gametes are specialized cells. The ovum is a gorged cell in which metabolic activity comes almost to a standstill—a cell that

must be activated in some way in order to produce a new individual. As a rule, activation is accomplished by another specialized cell, the spermatozoön, a tiny starved cell that uses up its store of energy-producing material in active locomotion and is doomed to die unless it finds the appropriate food supply furnished by the egg. Each kind of gamete thus furnishes what the other lacks, the egg supplying a large amount of inert energy-producing material and the sperm furnishing the additional energy necessary to make this material available for growth and cell division.

Each gamete is also the bearer of heredity materials. It has already been shown that the diploid chromosome complement of the unmaturated germ cells is reduced during maturation to the haploid chromosome complement, and that the union of two gametes to form a zygote reinstates the specific diploid chromosome complement. Thus we see that the process of fertilization, or union of gametes, has two distinct values: it serves to initiate development in the inert ovum and it furnishes a means of uniting the hereditary characters of two different genetic stocks.

Sexual or Gametic Reproduction in the Protozoa.—The process of gametic reproduction in the Protozoa is believed to be essentially the same process and to have the same significance as it has in the Metazoa. It differs, however, from the latter in that the whole unicellular body is at once somatic and germinal, for there are no separate germ cells. This means that, for a series of generations during which binary fission is going on, the somatic phase of the life cycle is in the ascendancy; but when the period of conjugation intervenes and cells fuse with each other wholly or in part, the germinal phase is in the ascendancy and the cells are essentially gametes. In a sense, then, we may say that, in these Protozoa, many generations of somatic individuals are followed by one generation of gametes and that there is an alternation of generations. In many species of Protozoa, especially among the Mastigophora, the gametes are alike in size and appearance. If any difference exists, it must be of a subtle physiological, rather than of a grosser morphological sort. Between this condition of ISOGAMY, where gametes are visibly alike, and the condition of HETEROGAMY, where the gametes are typical eggs and sperms, there is a long series of intermediate conditions showing stages in the differentiation of gametes of the two sexes. In all these types of gametic reproduction in the Protozoa so far cited there occurs complete fusion of

both nucleus and cytoplasm of one gamete with those of another—a union of entire cells.

Gametic Reproduction in Paramecium.—In Paramecium, however, and in a large number of other infusorians, gametic reproduction takes on a more specialized aspect. Let us recall for a moment the events of conjugation where there is only a temporary association of two individuals accompanied by an exchange of nuclei. After two preliminary divisions of the micronucleus, which simulate the maturation divisions of the metazoan germ cells, the remaining nucleus divides unequally into a larger stationary nucleus, resembling the egg nucleus, and a smaller migrating nucleus, resembling the sperm nucleus. The smaller nucleus of each individual migrates across the protoplasmic bridge into the other individual and fuses with the larger nucleus of the other individual. This closely resembles the behavior of male and female nuclei in metazoan fertilization. We may now ask ourselves whether the conjugating Paramecia are gametes or whether only their nuclei play the rôle of gametes. This difficult question cannot be satisfactorily answered, but the results of the process appear to be the same as in the Metazoa, for there is a renewal of growth and division energy and a new combination of hereditary materials is produced.

7. *Parthenogenesis*

This mode of reproduction may be defined as the development of ova without union with spermatozoa. Leading authorities consider parthenogenesis as a phase of gametic reproduction, for the ovum undergoes one or two maturation divisions, sometimes reducing the number of chromosomes and sometimes not. That parthenogenetic ova really are potential gametes is seen in cases such as those of the bees and wasps, in which all eggs are capable of development whether fertilized or not. If any egg happens to be fertilized, it produces a female (a sterile worker or a queen), while all unfertilized eggs produce males, or drones. Furthermore, many types of eggs that normally require fertilization may readily be induced to develop without fertilization by the use of simple chemical or merely mechanical stimulation, a process known as ARTIFICIAL PARTHENOGENESIS. We may then conclude that parthenogenesis is not just an archaic asexual mode of reproduction, but a modern specialization of the gametic type.

8. *Pædogenesis*

While not strictly a mode of reproduction comparable with or contrasting with those already described, pædogenesis is a widespread and interesting reproductive phenomenon. Typically, reproduction is a phenomenon of old age, or more accurately, of SENESCENCE. So long as an individual is physiologically young, is carrying on all of its activities at a high metabolic level, and has no blocks in its system of communications between controlling centers and outlying parts, it cannot reproduce, for reproduction means that some part of the body has lost its relations with the parent organism. When the organism grows physiologically old, some of its outlying regions fail to receive the integrational stimuli necessary for holding them in subordination to the central government of the parent body, and they become physiologically isolated. If they are to live at all, they must become new individuals. This is true whether reproduction is by fission, budding, twinning, sporulation, or gamete formation. Reproduction ordinarily does not occur until maturity or even old age, but there are many cases of precocious reproduction, young being produced during larval or embryonic stages of the parents. We can account for such cases only by assuming that these apparently young parents are physiologically old—senescent. When reproduction, especially that involving gametes, takes place in embryonic or larval stages, the phenomenon is termed pædogenesis (meaning literally reproduction by young). We recognize both parthenogenetic and bisexual (syngamic) pædogenesis.

Allied to pædogenesis is the phenomenon of NEOTENY as exemplified by the AXOLOTL LARVA of the tiger salamander, *Amblystoma tigrinum* (Fig. 256). In the mountain lakes of Mexico and New Mexico these larvæ, while still in possession of their external gills and other larval characters, become sexually mature and produce young. This, it will be noted, is a case of pædogenesis associated with bisexual or syngamic reproduction. Pædogenesis is also found to occur in parthenogenetic forms. A good example of this combination is that of MIASTOR, a species of fly belonging to the family Cecidomyidæ. This fly, while still in the larval condition and before oviducts for the escape of eggs have been differentiated, produces young in the body cavity. This generation of grublike larvæ escapes from the body of the infant mother by boring through

the body wall. Several generations are produced in this fashion, but finally a generation is produced that goes through the larval and pupal stages without reproducing, emerging as full-fledged males and females that reproduce in the usual way.

Another striking instance of pædogenesis associated with parthenogenesis is that of the liver fluke (*Fasciola hepatica*), the life history of which has already been described in another connection (Fig. 134). It may be recalled that the very young larva of this species, the miracidium, forms a sporocyst, within which a number

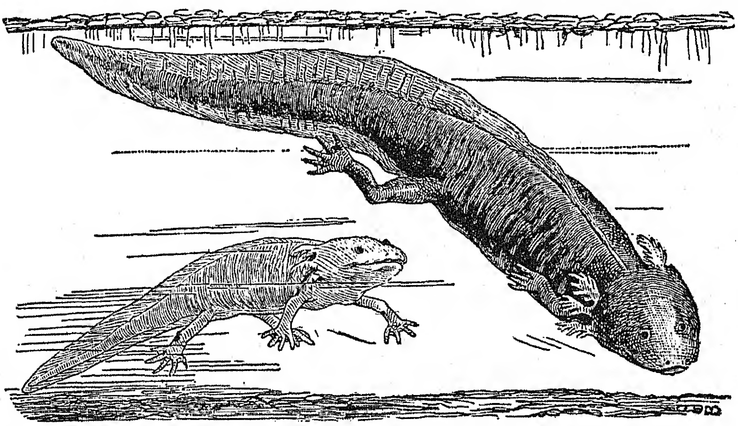


Fig. 256. Axolotls or larvæ of *Amblystoma tigrinum*. $\times \frac{1}{2}$. (From the Cambridge Natural History.)

of ova are produced. These ova undergo maturation and develop parthenogenetically into redia larvæ. These in turn produce more redias in the same fashion, and several successive generations of redias are produced one from another. Finally a generation of redias produces parthenogenetically a generation of cercarias, that grow directly into adult liver flukes if they are lucky enough to be eaten by a sheep.

9. *Hermaphroditism*

This phenomenon is to be thought of not strictly as a separate mode of reproduction, but as a complication arising out of gametic reproduction. It is also, we believe, not a relic of an archaic condition, as some authors suppose, but a relatively modern or cenogenetic condition commonly developed in connection with racial senescence in forms that have sedentary and parasitic habits.

When the sexes are separate, we speak of the condition as diœcious; when both sexes are represented in one individual, whether simultaneously or in succession, the condition is monœcious and the result is hermaphroditism (a compound word made up of Hermes and Aphrodite).

No better examples of this phenomenon could be given than those already described for Hydra, Planaria, the liver fluke, and the earthworm. In some cases hermaphroditism is associated with self-fertilization; in other cases, with cross fertilization. In forms that live an isolated parasitic life, self-fertilization seems to be the only feasible method; but when hermaphroditic forms are either somewhat mobile or live in colonies, cross fertilization is possible and is usually adopted; for the advantages of continually bringing together different genetic lines outweigh the advantages of somewhat more ready fertilization.

Many interesting combinations of the various modes of reproduction exist, but we have noted enough examples to gain some realization of nature's mechanisms for preserving the continuity of life.

SUMMARY

1. Among those mechanisms that play an important rôle in racial maintenance and adjustment are reproductive mechanisms.
2. E. B. Wilson classifies modes of reproduction broadly as *a*, somatogenic and *b*, cytogenic. Somatogenic reproduction includes all cases in which a part of the parent body other than germ cells gives rise to offspring. Cytogenic reproduction is accomplished by means of single cells released from the parent body, and includes both spore reproduction and reproduction by gametes.
3. Transverse fission was seen in Planaria and in Paramecium; lateral budding in Hydra, etc.; longitudinal fission in Euglena and in duplicate twins in the armadillo and in man; internal budding in sponges, etc.
4. Spore reproduction was seen in the Class Sporozoa; and gametic reproduction in all Metazoa and in some Protozoa.
5. Parthenogenesis is regarded as a degenerate form of gametic reproduction.
6. Pædogenesis was noted in the life history of the liver fluke. The phenomenon involves gametic (or parthenogenetic) reproduction by embryos or larvæ. It may be regarded as a consequence of precocious sexual maturity.
7. Hermaphroditism was noted in sponges, hydra, flatworms, earthworms, tunicates, and other sessile or sedentary organisms. It is common among parasites. It seems to be an adaptation permitting sexual reproduction in organisms that might have difficulty in mating.

CHAPTER XLIV

ORGANIC EVOLUTION

(INTRODUCTORY STATEMENT)

A. Importance of the Concept of Evolution

The principle of evolution is so all-pervasive that it touches in some respect practically every aspect of biology. Hence, at least by implication, evolution has been a matter of central interest throughout this whole book. It must be obvious to any student that the mere classification of animals into phyla, classes, orders, families, genera, and species implies evolution, for the resemblances that make it possible to group organisms into any of these assemblages are explained as inheritances from a common ancestor. Classification is quite meaningless on any other grounds. In this connection it should be recalled that the order of treatment of the various animal phyla is largely determined by the Diphyletic Tree Theory, a new scheme for expressing the main lines of evolutionary change in the Animal Kingdom. Thus the evolution concept runs like a complex pattern throughout the whole fabric of biological science.

Although, as has been said, evolution has been a guiding principle throughout this book, there has been as yet no adequate discussion of those special facts and theories that are specifically evolutionary. It is our purpose in the remaining chapters of the book to present in an orderly and logical way the main facts and theories that constitute the subject of evolutionary biology.

The plan to be pursued is as follows:—First, we intend to present the evidences of evolution, upon which the validity of the theory largely rests; and second, we shall describe the various causal mechanisms involved in the process. It is now definitely known that the primary mechanisms of evolution are cell mechanisms, especially those having to do with the chromosomes of germ cells. Hence it is important to consider in detail the mode of origin of germ cells, the peculiar mechanisms involved in the production of gametes, the process of union of gametes to form zygotes, sex

as a factor in evolution, how sex is determined, the rôle of chromosomes in heredity and variation, and the laws of heredity that are the result of the known regularities in the operation of chromosomal mechanisms. In a final chapter the causal factors of evolution are discussed in relation to one another, and an attempt is made to show how they are all essential and all work together as parts of a single complex mechanism.

B. The Nature of the Proof of Organic Evolution

Although it is still customary to speak of the Theory of Evolution, one must not assume that the word "theory" implies uncertainty. We still speak of the Cell Theory, though the implications of this great generalization are quite unquestioned. The Theory of Evolution rests on the same kinds of evidence as do other great scientific generalizations. It is supported by as extensive and as strong evidence as are the Law of Gravitation, the Law of Conservation of Energy, the Law of Uniformitarianism, the Atomic Theory, and others. All of these are no more than explanations of how nature works. The proof of their validity depends upon how satisfactorily these explanations continue to account for the facts within their range of application.

Now the nature of the proof of evolution is this: that using the idea of evolution as a working hypothesis, it has been possible to rationalize and explain a vast array of observed phenomena, the real facts upon which evolution rests. Thus classification, comparative anatomy, embryology, blood tests, palæontology, geographic distribution, and genetics, become consistent and orderly branches of science when based on evolutionary foundations, but when viewed in any other way they are thrown into the utmost confusion. There is no other explanation of organic phenomena that is of the least service in giving these bodies of facts any sort of scientific coherence or unity. In other words, the working hypothesis of Organic Evolution does all that can be asked of it and is therefore worthy of credence, at least until a better hypothesis appears to take its place. No rival hypothesis of a scientific nature is in sight, and none is likely to appear, for confidence in the validity of the Theory of Evolution is increasing year by year. The theory not only serves admirably as a working hypothesis that never fails to work, but with the steady accumulation of more and more facts, the weight of evidence is now so great as to overcome

all open-minded opposition by its sheer mass. In the next chapter a limited sample of the evidences supporting evolution will be presented.

SUMMARY

1. The general principle of organic evolution is a master principle of biological science. Almost every phase of biology has its evolutionary aspects.

2. Biology has become an organized science largely because it is based upon the principle of evolution.

3. Like any other scientific principle, the validity of the Theory of Organic Evolution depends on the evidences that support it.

4. Two kinds of evidence are available: *a*, historical and *b*, experimental. Historical evidences prove that evolution has occurred in the past, while experimental evidences show that evolution is going on today. The two kinds of evidences taken together indicate that evolution is a continuous process.

5. Palæontology is direct historical evidence, while classification, comparative anatomy, embryology, blood tests, and geographic distribution are indirectly historical in character, since they afford information as to ancestral relationships.

6. Genetics is essentially experimental and affords evidence about evolution going on today, but by inference suggests the modes of evolution that probably prevailed in the past.

7. All these fields afford evidences for organic evolution, because, when they are studied in the light of evolution, they become intelligible and rational subjects, that support one another and focus on but one conclusion—that organic evolution is a fact.

CHAPTER XLV

EVIDENCES OF EVOLUTION

THE main bodies of biological data that are rationalized by and therefore support the Principle of Evolution are the following:—

1. Comparative anatomy.
2. Classification.
3. Blood tests.
4. Embryology.
5. Palæontology.
6. Geographic distribution.
7. Genetics.

A. EVIDENCES FROM COMPARATIVE ANATOMY

a. The Principle of Homology.—A general survey of the Animal Kingdom brings to light the fact that there are several distinct main types of architecture, each of which characterizes one of the grand divisions of the Animal Kingdom. Within any one of these grand divisions there are all kinds of structural diversities, but in spite of this the fundamental plan is obvious. The situation reminds one of the variations upon a theme in music: no matter how elaborate the variations may be, the skilled musician can recognize the common theme running through it all. This fundamental unity of architecture underlies the principle of homology and is the basis of comparative anatomy as well as of other branches of morphology.

Homologous structures are those that arise from similar embryonic rudiments and have equivalent relations to other structures. Homology has nothing to do with the function of the organ nor with the superficial adaptive features of it. If we examine the arm of man, the flipper of a whale, the wing of a bird or that of a bat, the foreleg of a horse or that of an ox, we may not see at first any similarity, but a detailed study of their anatomical make-up reveals a surprising amount of resemblance (Fig. 257). We find the same bones, muscles, nerves, but differing in size, proportions, and degree of development. Although the plan of structure is the same

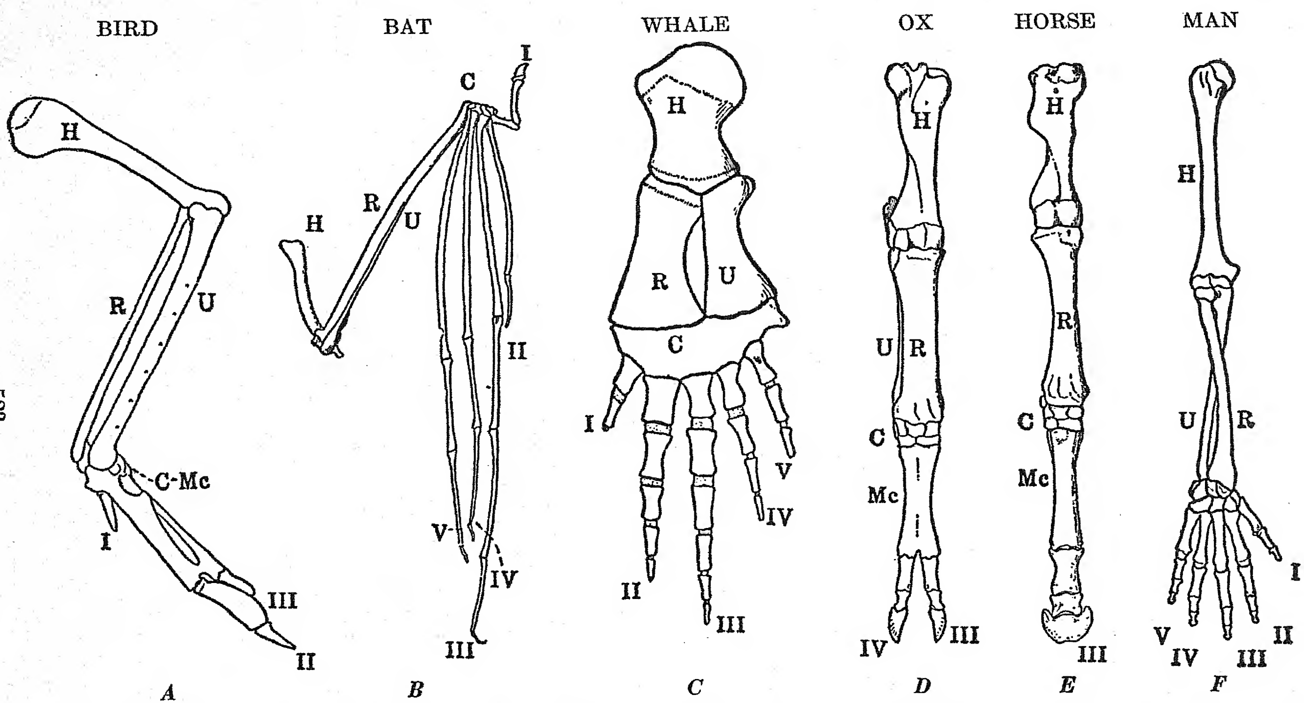


FIG. 257. Vertebrate fore limbs to show homologous skeletal structures. *A*, left wing of a bird (Raven); *B*, right wing of a bat; *C*, left flipper of a whale; *D*, right foreleg of ox; *E*, right foreleg of horse; *F*, right arm of man. C, carpals; H, humerus; Mc, metacarpals; R, radius; U, ulna; I–V, digits. (From Scott.)

in all, the variations upon the plan are very different and are of such a character as to render the organs especially useful for various purposes: flying, swimming, or general versatility. The Principle of Evolution rationalizes this situation. The reason why all these organs, so diversified in appearance and in uses, have a common ground plan is that they have all inherited their main structural features from a common ancestral group, but each has undergone a different sort of adaptive modification. This is merely a paraphrase of the Principle of Evolution.

b. Vestigial Structures.—Even more in need of an evolutionary explanation than ordinary homologies are those homologies termed

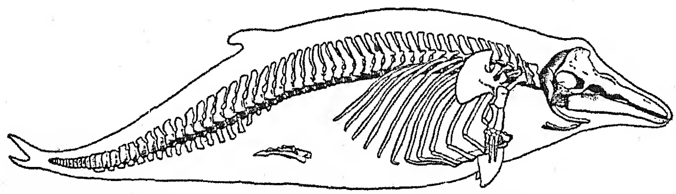


FIG. 258. Skeleton of porpoise (a small whale). The vestigial pelvic bones are shown embedded in the flesh. (From Lull, after Pander and D'Alton.)

vestigial structures. In the foreleg of the horse, for example, there are two little bones, shaped like toothpicks, lying closely applied to the two sides of the metacarpal bone. These have no known function and would be meaningless were it not for the principle of homology. These tiny vestiges are now recognized as the last remnants of the second and fourth toes, the homologues of which were well developed in many extinct species of horses.

Whales furnish another classic instance of vestigial structures. Deeply imbedded under the blubber in the pelvic region of the body is a little handful of bones (Fig. 258) that are totally immovable and cannot possibly function as bones at all. Yet there is no question but that they represent all that remains of the pelvic girdle and the hind legs. This being the case, the only possible inference is that the whale has been derived by descent from an ancestor that had functional hind legs.

There are, according to ***Wiedersheim,*** no less than 180 vestigial structures in man—enough to make the human body a veritable walking museum of antiquities. Among these are: the vermiform appendix, the abbreviated tail, a whole set of useless caudal muscles, muscles for moving the ears, miniature third eyelids, a com-

plete coat of hair (lanugo) on the embryo, and a long list of others. All of these are represented among lower types of animals by functional homologous organs. The only reasonable interpretation of these vestiges is that man has descended from ancestors in which these structures were functional. Man has, as a matter of fact, never completely lost these inherited structures though they may no longer be of any value. They exist in man's body because of the stubbornness of heredity, which seems to cling persistently to some expression of all that the race has once possessed, even though chiefly concerned in the elaboration of its more recent adaptive acquisitions.

The fundamental assumption underlying the principle of homology is that homologies are due to heredity; that unity of type implies common ancestry. We have ample proof that structural resemblances are due to heredity. Studies of identical twins and of armadillo quadruplets strongly support this contention, for in both of these cases the closest known resemblance is associated with the fact that, being products of a single egg, they have the most nearly identical heredity possible. *Real homologies are inherited similarities.*

c. **Homology versus Analogy.**—It is not uncommon to find structures that look alike and function alike but are not homologous. Thus, the eye of the squid, a cephalopod mollusk, has a chorion, a lens, a retina, an optic nerve, and a general aspect very like the eye of a fish. It also functions in the same way as a vertebrate eye. A study of its embryonic development, however, shows that not in a single particular is the eye of a cephalopod homologous with that of a vertebrate. The two eyes are ANALOGOUS, not homologous. They are the result of the convergent adaptation of quite different materials to subserve a common function—that of vision. HOMOLOGOUS structures, on the other hand, are frequently, though not always, adapted for quite different functions, and in accord with this they may exhibit great differences in form and in superficial appearance. Yet, in spite of the greatest divergence in form and function, structures are homologous if they arise from equivalent embryonic rudiments and have equivalent morphological relations.

Both analogy and homology imply change in structure and in function in relation to environment, and in that way they plainly suggest adaptive change in organisms. This, in turn, implies evolution.

Comparative anatomy then rests upon an evolutionary foundation, and is a science only in so far as it makes use of the principle of homology, a corollary of evolution.

B. Evidences from Classification

The object of classification is to arrange all animals and plants in groups of various degrees of inclusiveness, which shall express as closely as possible the actual degrees of relationship existing between them. Accordingly, we put into one group all animals that are alike or are essentially of the same kind; and we call such an assemblage a SPECIES. Thus, the European wolf is a species and has been designated *lupus* (the Latin word for wolf). There are also several other species of wolf, each with its Latin name, and all of these are grouped with dogs—believed to be domesticated wolves—into a group, or GENUS, called *Canis* (the Latin word for dog). Several other genera (the plural of genus), made up of assemblages of such doglike animals as the foxes and the jackals, are placed with the genus Canis in a larger group called the FAMILY Canidæ—meaning the Dog Family. The assumption underlying this grouping is that all animals within the Family have been derived from some common doglike ancestor. Other families, such as the Felidæ (Cat Family), Ursidæ (Bear Family), and several other families of terrestrial beasts of prey, are grouped with the Canidæ into the SUBORDER Fissipedia. These, in turn, are grouped with the marine beasts of prey—seals, sea lions, and walruses—into the ORDER Carnivora. Several other orders of beasts, such as Insectivora, Rodentia, Primates, Ungulates, Cetacea, and others, constitute the CLASS Mammalia. The latter (together with several other classes such as Pisces, Amphibia, Reptilia, Aves) make up the SUBPHYLUM Craniata (Vertebrates), which (together with several assemblages of vertebrate-like forms) comprise the PHYLUM Chordata.

The underlying assumption of classification is the same as that which underlies comparative anatomy: that degrees of blood relationship run strictly parallel with degrees of true resemblance; that the most nearly identical individuals are the most closely related and that those bearing the least fundamental resemblance to each other are either unrelated or, at the most, descendants of an extremely remote common ancestral type. The assumption is merely an affirmation of the fact of heredity: that like tends to

produce like. The validity of the principle of heredity has been demonstrated in so many ways that it needs no justification here.

Let us examine somewhat critically the content of the unit of classification—the SPECIES. When we look over a large number of individuals of the same species, we find that no two of them are exactly alike in any one or more respects. As a rule, there is a wide range of diversity within a species, and extreme variants are often very different from one another. The several species of a prosperous genus are often so variable that it becomes a matter of great difficulty to determine just where one species stops and another one begins. Moreover, it sometimes happens that some of the individuals occupying extreme parts of the range of the species are so different from the central type that they would doubtless be diagnosed as belonging to a different species were it not for the fact that all intergrades between the extremes are known to exist. A species is, therefore, rarely a fixed and definite assemblage, such as it should be if species were specially created and had not evolved. In fact, any intensive study of a species gives the impression of a vast network of interrelated individuals changing in all sorts of ways.

When we have finished classifying a group of animals such as the vertebrates, we find that we have a sort of treelike arrangement. The phylum, one of the major branches of the tree of life, divides into several somewhat smaller branches, the classes. The classes divide into orders, the orders into families, the families into genera, the genera into species, the species into subspecies, varieties, or races, which may be looked upon as the terminal twigs. This treelike arrangement is just what we would expect to find in a group descended from a common ancestry and modified along many different lines. If all this is the result of special creation, it is indeed unfortunate that it speaks so plainly of descent with modification, which is none other than evolution.

C. Evidences from Blood Tests

There is another way of classifying animals: on the basis of chemical similarities in their blood. It is known that the blood of an animal contains certain materials that are even more sharply specific than are its structural peculiarities. These blood elements form the basis for an extremely delicate means for testing organic relationships. Thus, if we wish to find out which animals have a

blood resemblance to man, we proceed in the following fashion: Human blood is drawn and allowed to clot, thus separating the solid from the fluid constituents. The watery fluid—the serum—contains the specific human blood elements and is the material used in all of these experiments. Small doses of human serum are injected intravenously into a rabbit—any other mammal would probably do as well—and the injections are repeated at intervals of about two days until the rabbit is considered thoroughly sensitized. At first the injected animal is more or less sickened by the foreign material in its blood, but before long it shows no ill effects. What has happened is that the rabbit's blood has reacted to the presence of human serum in such a way that the latter is neutralized. The specific neutralizing substance is termed an ANTIBODY. Serum of the experimental rabbit contains much of this substance and is therefore called antihuman serum. Now, if a quantity of this antihuman serum be mixed with human serum, a heavy white precipitate is formed. When antihuman serum is mixed with serum of any of the anthropoid apes, the precipitate is somewhat less abundant and takes longer to form, but is very positive in character. The tests, however, reveal a less prompt and abundant reaction with the sera of other Primates. The strength of the reaction runs strictly parallel with the supposed relationships based upon homologies. "It is a remarkable fact," says ***Nuttall,*** "that a common property has persisted in the bloods of certain groups of animals throughout the ages which have elapsed during their evolution from a common ancestor, and this in spite of differences of food and habits of life. The persistence of the chemical blood-relationship between the various groups of animals serves to carry us back into geological times, and I believe we have but begun the work along these lines, and that it will lead to valuable results in the study of various problems of evolution."

The tests carried out with other groups of animals showed a remarkable, though not mathematically exact, parallelism between the relationships revealed by this new technique and those that had been previously worked out by the older methods. Many relationships that were obscure to the morphologists seem obvious to the serologist, for blood tests of relationships are more sensitive than are those based on homologies. Had blood tests and homologies failed to agree, our faith in the validity of both would have been severely shaken; but they are in essential agreement—a fact

that greatly strengthens our confidence that they both speak truthfully about the descent of different animal groups from common ancestors.

D. Evidences from Embryology

There should really be no sharp distinction between evidences from comparative anatomy and those from embryology. The two branches are inseparable: one must be interpreted in the light of the other. Comparative anatomy ostensibly deals with the structures of adult organisms; but whenever there is any question as to obscure homologies, recourse is had to an embryological investigation of the relations of the structures in question. If it is found that the further back the two structures are traced the more closely do they approximate each other and that ultimately they are traced back to homologous embryonic primordia, the relationship of the structures in question is believed to have been established. We cannot be certain of homologies until confirmed by embryological study.

It should always be remembered that an individual is not merely the last stage of its development, but that it includes also the whole ontogeny from the egg stage till the end of life. Very closely related individuals will keep step all the way through their developmental stages, diverging only slightly at the end; distantly related types diverge comparatively early in their developmental paths; while unrelated types may be different from the beginning. The most advanced groups of organisms travel a much longer journey before reaching their destination than do the simpler organisms. In many instances certain early stages in the development of an advanced type resemble in unmistakable ways late stages of less advanced types. This apparent repetition in the development of the higher organisms of conditions characteristic of some of the lower organisms has so impressed certain biologists that they have come to the conclusion that *the development of the individual may be regarded as an abbreviated repetition of the ancestral history of the species*. This conception has taken shape as the Biogenetic Law, or the Law of Recapitulation.

Attractive as it sounds, there is reason for serious doubt as to the validity of this generalization. In the first place, we know that no embryonic stage, as a whole, is equivalent to any adult organism of a lower order. While it may have some characters strongly rem-

iniscent of those of adult structures of lower groups, the *tout ensemble* is not at all like the latter. Again, developmental stages must be adapted to the environment at all times, and therefore acquire many embryonic or larval organs that are of the utmost importance for the maintenance of individual life but have no ancestral significance at all. Furthermore, different systems of organs develop at entirely different rates according to the immediate necessities of the particular case. In some forms, for example, the nervous system may be far along its course of differentiation before the circulatory system has even begun to differentiate. No adult ancestor is likely to have had so discordant an organization.

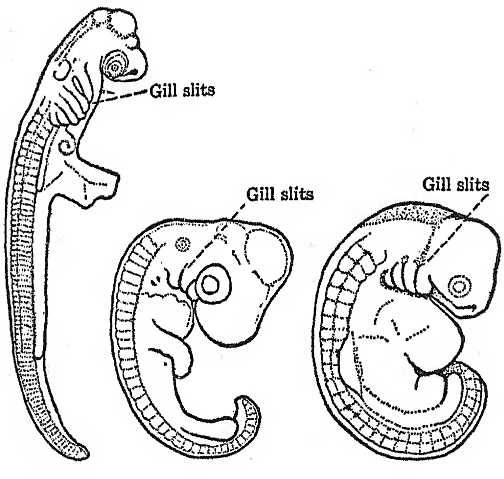


FIG. 259. Embryos in corresponding stage of development.

In spite of its shortcomings, however, the idea that *ontogeny recapitulates phylogeny* is a very useful tool in the hands of the skilled embryologist, who realizes the chances of error and applies the principle in critical fashion. As an example of the legitimate use of the principle of recapitulation let us consider for a moment the following case: The circulatory system of a man passes through a condition closely paralleling, first, that of a fish, then that of an amphibian, then that of a reptile, and finally reaches the typical mammalian condition. Again, we find that the human embryo closely resembles the fish in having gill slits (Fig. 259) which never function as such, but become either obliterated or else remodeled so as to be scarcely recognizable for what they are. Thus one pair of gill slits in man has been transformed into the Eustachian tube, the middle ear and the external ear passage, parts of the complex mechanism of hearing.

An example of what is generally regarded as a legitimate use

of the recapitulation concept is afforded by the larval development of some of the higher crustacea belonging to the subclass Malacostracha. Many members of this group have complicated life histories involving several distinct larval types quite different

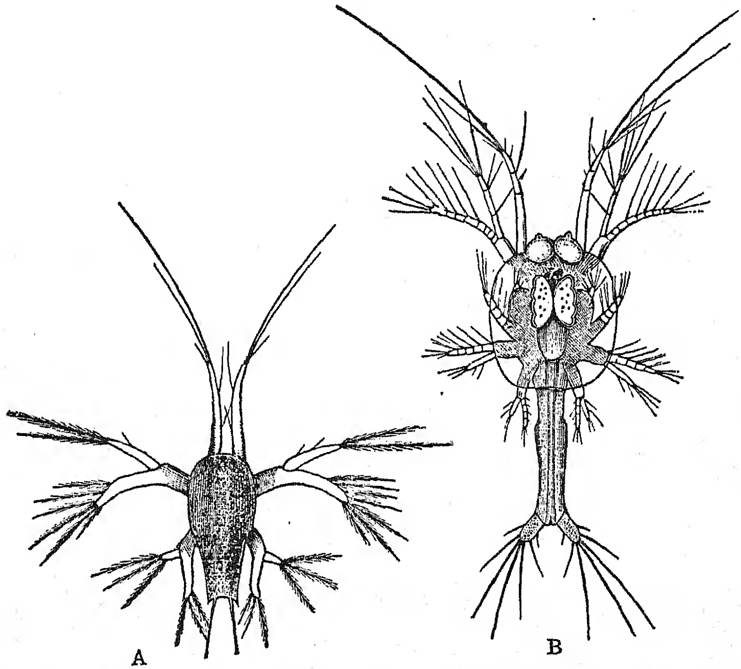


FIG. 260. Two stages in the development of the shrimp, *Penæus*. A, *Nauplius* stage. B, *Protozoæa* stage. (From Sedgwick's Zoology, after Fritz Müller.)

from one another. Thus the shrimp, *Penæus*, hatches from the egg as a *Nauplius* larva, characterized by having a single median frontal eye and only three pairs of appendages (Fig. 260, A). In this condition it resembles such primitive crustaceans as the copepods. The Nauplius molts and is transformed into a second larval type, called the *Protozoæa* stage (Fig. 260, B), which possesses six pairs of appendages and the beginnings of segmentation. The Protozoæa molts to produce the *Zoæa* stage (Fig. 261, A) which rather strongly resembles the adult Cyclops, another primitive crustacean. The *Zoæa* grows and molts to form the *Mysis* stage (Fig. 261, B) with thirteen appendages and a cephalothorax, a stage strongly reminding one of the adult Mysis, a member of a

group somewhat more primitive than the shrimps. The Mysis stage then molts to give rise to the juvenile shrimp. Thus the shrimp, in the course of its ontogeny is believed to pass through several developmental stages resembling in a general way the

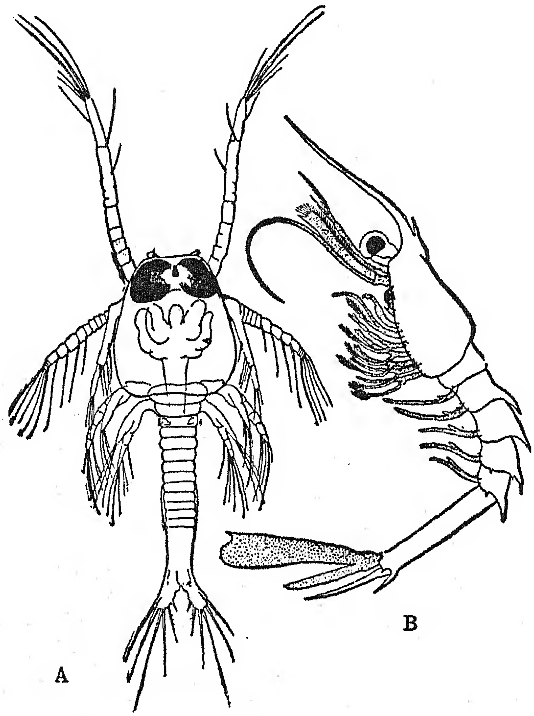


FIG. 261. Two later stages in the development of *Penæus*. A, *Zoæa* stage. B, *Mysis* stage. (From Korschelt and Heider, after Claus.)

conditions of several grades of living lower crustaceans that might be considered as quite like the ancestors of the shrimps.

An even more striking instance of the apparently proper use of the recapitulation theory is found in connection with another group of Crustacea, the Cirripedia. In the adult stages these animals, barnacles and Sacculina, are sessile, degenerate forms or extreme parasites.

Barnacles as adults have long been known, for they form curious shelly incrustations on the bottoms of ships, on piles, and on rocks. They were in early times classified as molluscs and even as verte-

brates. Because of their oddity they were at one time placed in a distinct phylum. It was only when *J. V. Thompson* studied their embryonic and larval life that they were found to be crustaceans. They are now classified as members of the Subclass Entomostraca, and the Order Cirripedia has been created for them and their relatives. This order is peculiar in having as a first larva a NAUPLIUS, similar to that of other Entomostraca. The Nauplius, however, metamorphoses to form a second type of larva, known as CYPRIS, which is found only in the Cirripedia. The Cypris larva, after a short free-swimming life, settles down and becomes sessile, using its antennæ as anchors. It then undergoes a second metamorphosis, during which it takes on the peculiar characters of the adult barnacle with its mantle and shell and reduced head.

Years after the true relationships of the barnacles had been discovered there was found a strange parasitic growth, called SACCULINA, resembling a tumor, attached to the body of a certain kind of crab (Fig. 262, **C**). It consisted of a sort of soft sac with numerous rootlike processes invading the crab's body. It bore no resemblance to anything else in nature and was therefore a complete mystery until its eggs were discovered and its embryonic history worked out. It then proved to be a relative of the barnacles; for it had both the Nauplius (Fig. 262, **A, B**) and the Cypris larva as well as the habit of settling down upon its antennæ. But, instead of settling down and becoming merely sessile, as do the barnacles, it becomes profoundly parasitic. When the Cypris settles down, it thrusts its antennæ into a hair follicle of a crab; then its body tissues become disorganized into a fluid condition resembling a cellular emulsion. This flows through the hollowed-out antennæ into the blood spaces of the crab. There the loose cells round up into a ball-like mass that floats about in the blood of the crab until it reaches the intestine of the host, where it fastens itself by rootlike processes and lives parasitically upon the body fluids surrounding it. This almost formless parasite then reveals itself through its embryology to be a still more profoundly degenerate relative of the degenerate barnacles and, through the latter, a descendant from the free-living crustaceans.

These are only isolated examples of the ways in which the principle of recapitulation, when properly used, aids in the work of classification. They also serve to emphasize the fact that, in the hands of the trained expert, the evidences of evolution as de-

rived from embryology are perhaps the most convincing evidences we have; whereas, in the hands of overenthusiastic or uncritical

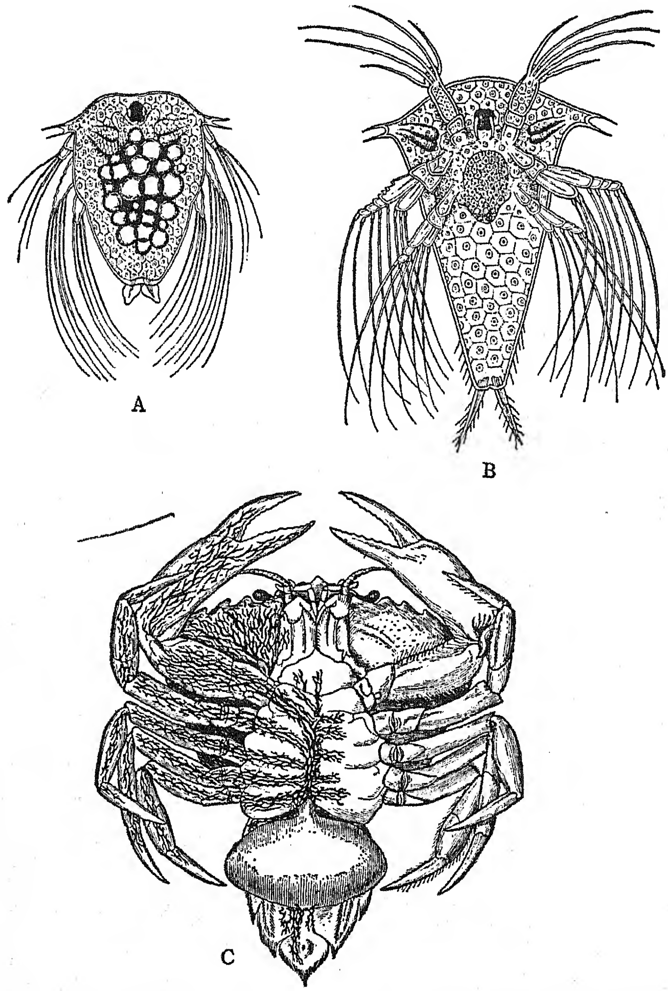


Fig. 262. The nadir of parasitism, *Sacculina carcini.* A and B, larval (nauplius) stages; C, crab, *Carcinus mænas,* with a mature *Sacculina* in situ, showing ramifying "roots" (omitted from right side) which extract nourishment from the crab. (From Lull, after Delage, from Leuckart.)

amateurs, they become decidedly treacherous and dangerous playthings. The literature of evolution is full of false inferences based

upon inadequate embryological data, and this has done much to destroy confidence in the whole body of embryological evidence.

E. Evidences from Palæontology

1. *The Incompleteness of the Record*

Palæontology is the science of ancient or extinct life. Its materials are the fossil remains of animals and plants that once were living. Fossils are real; they cannot be explained away. If evolution has taken place and sample specimens of all of the animals and plants that ever lived were available for study, we should be able not only to prove the fact of evolution, but to show exactly the courses it has followed. Even if every specimen were labeled with the geographic locality where it was found and with the geological period when it lived, it would still be a staggering task to unravel all of the interwoven lines of descent. If, even with a complete fossil record, the task of reconstructing the history of the evolution of organisms would be a difficult one, how much more difficult must we expect to find this task when we realize how very incomplete the record really is!

The best of reasons exist why the palæontological record must forever be, at best, interrupted and fragmentary. In the first place, a very large proportion of the lower strata of the earth—strata that must have once contained the fossils of the oldest forms of life—have been so modified by heat and pressure that all traces of fossils have inevitably been obliterated. In the second place, enormous masses of fossil-bearing rocks have been destroyed by the eroding effects of rainfall and rivers, waves and glaciers. In the third place, only a small fraction of the fossil-bearing rocks are as yet, or are likely ever to be, available for study. Finally, the chances of an animal dying under such circumstances that its body would be preserved as a fossil are so small that only representatives of populous and widely distributed species are likely to have been preserved at all.

2. *Different Kinds of Fossils*

Several different sorts of fossils are distinguished:—

a. Dead and Preserved Bodies.—The actual dead and preserved bodies, or parts of bodies, of animals or plants, with the original tissues intact, and inclosed either in ice or in amber (Fig. 263), or

else mummified in various ways, form one class of fossils. Thus there have been recovered from the arctic ice or from the permanently frozen soil the still fresh bodies of mammoths, dead probably thousands of years. Again, many extinct species of in-

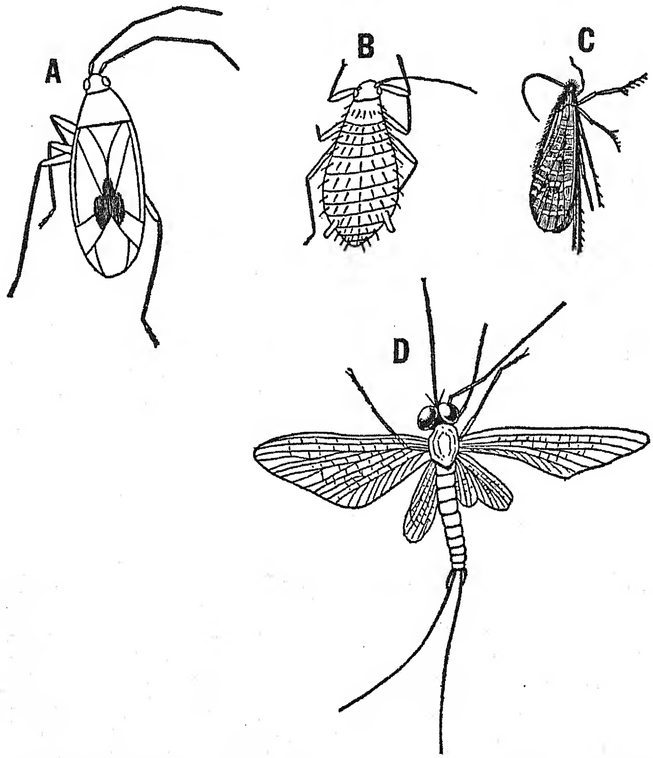


FIG. 263. Insects preserved in amber. A, bug; B, aphid; C, caddice-fly; D, may-fly. (From Lull, after Neumayr.)

sects have been preserved with the utmost faithfulness in amber, a transparent, petrified, resinous gum.

b. Petrified Fossils.—This type is important and numerous. In these fossils, organic matter has been replaced, particle for particle, by mineral matter in such a way that the finer structure of the tissues has been faithfully duplicated and rendered permanent.

c. Casts.—Perhaps the most numerous of all fossils are casts of animals. An animal or plant has lain in mud or clay long enough to have left its impress; the mud hardens about the body and forms

a mold; the organic matter disintegrates and the mold is filled with hard mineral matter; and the matrix may then be removed so as to leave the perfect cast.

d. Prints.—Prints and traceries constitute the last of the kinds of fossils to be dealt with. An animal walking in partially hardened mud may leave a footprint that becomes preserved when the mud hardens into rock. Traceries have been left in the lithographic stone quarries, representing the forms of jellyfishes or the delicate lacy wings of insects. These are as real as any other kind of fossil.

3. *How Fossils Are Formed*

The usual conditions of fossilization involve the death of the animal under such conditions that the body lies in water where it may rapidly be covered with sediment. The mouth of a river during a flood would furnish such a situation. Animals drowned in the flood might readily be preserved in considerable numbers in this fashion. Marine organisms, at least those living along the coast or in shallow bays, meeting death in the water and falling to the bottom as they do, have naturally been preserved more abundantly than have terrestrial forms. Other animals have been preserved by sinking in quicksand, by falling into asphalt lakes, or by being covered up by sand drifts on the open plains or deserts.

4. *The Causes Underlying the Stratification of the Earth's Crust*

Geologists inform us that in early times the earth's crust was all hard and rocky, composed chiefly of granites, basalt, and other crystalline materials. This hard mass was gradually softened and disintegrated through the action of rain, sun, wind, and atmospheric gases. The loosened fragments were washed away by the rains and streams and deposited in depressions of various sorts, forming horizontal or stratified layers. Had the earth's surface been entirely rigid all irregularities would long ago have been leveled down and we would have a smooth surface; but the earth's crust has undergone a slow process of wrinkling, accompanied by uprisings in some parts and depressions in others. When a region becomes considerably elevated, as in a mountain chain or a high plateau, the tendency is for it to be worn down by erosion and for its materials to be deposited in the valleys or else to be carried by

rivers to the lakes or seas. A further wrinkling may elevate the low places and depress the high places, resulting in another shift of materials. In this way the earth's crust has been shifted back and forth. One stratum is sharply marked off from the next because of the fact that while an area is elevated, much of its thickness is washed away, bringing its deeper parts to the surface; and when this same area once more becomes depressed and begins to receive another layer of sediment, the type of sediment has changed in character and the organisms that die and become fossilized are many thousands of years more recent than those imbedded in the worn-down layer just below. This is one of the reasons why the fossils of contiguous strata so often appear to be so sharply different in character.

5. *The Age of the Earth*

According to the most recent estimates, based on the rate of radium emanation, 1,500,000,000 years have elapsed since the earth attained its present diameter. Various other estimates range from about one tenth of this figure to one considerably greater than that given. Calculations as to when life first appeared on the earth's surface give results varying from 50,000,000 years to twenty times that figure. The latter estimate is believed to be accurate within no more than 30 per cent error.

6. *The Geological Time Scale*

Geologists have subdivided the strata of the earth's crust into Eras, Periods, and Epochs. The accompanying table (Fig. 264) gives in concise form the data as to the ages of the various rock levels together with the characteristic fossils. It will be noted that only the upper half of the strata, beginning with the Cambrian, are fossil-bearing. The layers below that level are composed of igneous or metamorphosed rock. Only indirect evidences of the former existence of fossils below the Cambrian level are at hand, but there is every reason to believe that from one half to two thirds of the evolution of life had been completed prior to the beginning of the Palæozoic Era. About these earlier chapters in evolutionary history we shall probably never have any satisfactory information.

7. *The Main Facts Revealed by the Fossil Record*

(*a*) None of the animals or plants of the past are identical with those of the present. The nearest relationship is between a few

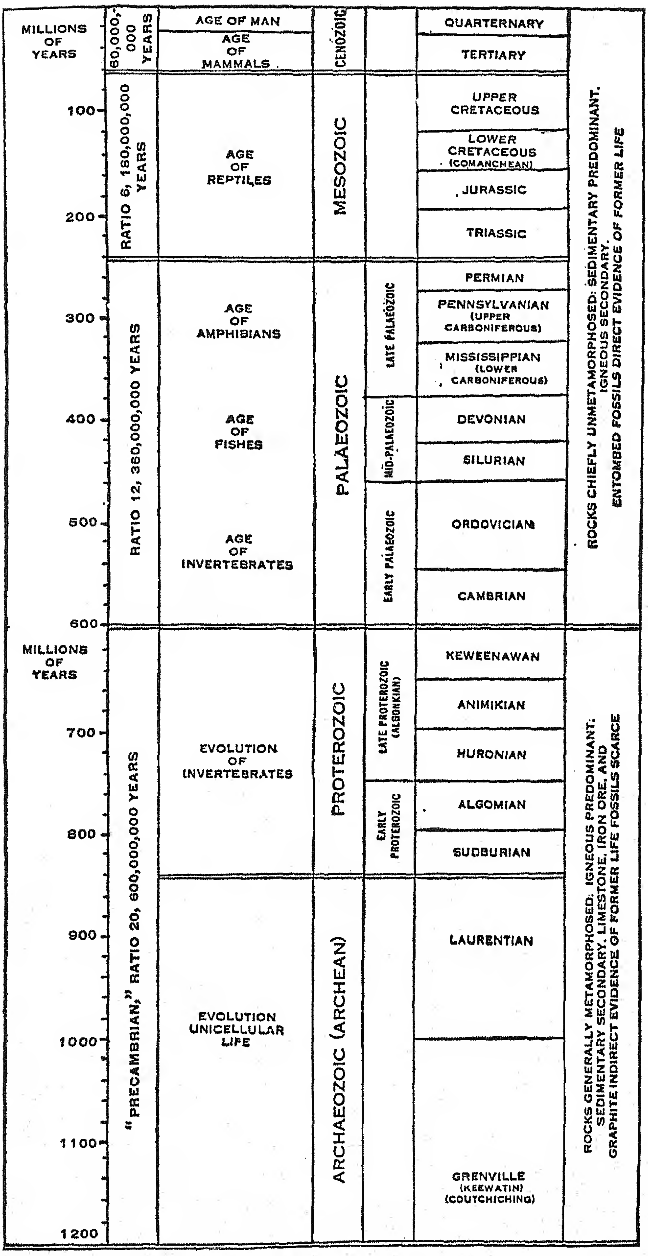


Fig. 264. Total Geologic Time Scale, estimated at 1,200,000,000 years. (From Newman, after Osborn, modified to agree with the more recent estimates.)

species of the recent past and some living species, which are sufficiently alike to be placed in the same genus.

(*b*) The animals and plants of each geologic stratum are at least specifically different from those of any other stratum, though in some cases they belong to the same genera.

(*c*) The animals and plants of the lowest geologic strata represent all of the existing phyla except the Chordata (vertebrates), but the representatives of the various phyla are relatively generalized, rather simple forms, as compared with modern representatives of the same phyla.

(*d*) The animals and plants of the uppermost strata are most like those of the present and serve as links between the present and the more remote past.

(*e*) There is to be seen a gradual progression from simpler and more generalized types toward more complex and specialized types as one proceeds from the lower toward the upper strata.

(*f*) Many groups of animals and plants have long ago reached the climax of their paths of specialization and have become extinct.

(*g*) Only the more generalized representatives of groups that, as a whole, have become specialized have succeeded in weathering the vicissitudes of changing world conditions and have survived up to the present.

(*h*) It is common to find a new group arising near the close of a geologic period during which great climatic changes were taking place. Such an incipient group almost invariably becomes the dominant and characteristic group of the next period, the probable reason for this being that the group in question arose in response to the conditions that were ushering in the new period and were therefore adapted to the new situation.

(*i*) The evolution of the vertebrate classes is more satisfactorily shown than that of any other group because they arose within the period of which we have a fossil record. Of the vertebrates, the history of the mammals is most complete, partly because they belong to relatively modern times and partly because the mammalian skeleton has been readily preserved in fossil form.

(*j*) Although many of the invertebrate phyla had already reached an advanced stage of evolution when we get our first glimpse of them in the Cambrian, many beautiful ancestral series

have been found that enable the palæontologist to describe in detail the courses of branching descent leading to the surviving types of today.

(*k*) Many complete fossil pedigrees, connecting specialized modern animals with much more generalized ancestors, have been worked out. Such pedigrees as those of the horse, of the elephant, of the camel, are classic instances. These essentially complete series afford perhaps the most convincing evidence at our disposal that evolution has taken place. A single example of this type of evidence will be given—that of the horse. Any one of several others would serve equally well.

8. *The Pedigree of the Horse*

As recorded by ***Dendy,*** the course of evolution of the horse family (Equidæ) "has evidently been determined by the development of extensive, dry, grass-covered, open plains on the American continent. In adaptation to life on such areas structural modification has proceeded chiefly in two directions. The limbs have become greatly elongated and the foot uplifted from the ground, and thus adapted for rapid flight from pursuing enemies, while the middle digit has become more and more important and the others, together with the ulna and fibula, have gradually disappeared or been reduced to mere vestiges. At the same time the grazing mechanism has been gradually perfected. The neck and head have become elongated so that the animal is able to reach the ground without bending its legs, and the cheek teeth have acquired complex grinding surfaces and have greatly increased in length to compensate for increased rate of wear. As in so many other groups, the evolution of these special characters has been accompanied by gradual increase in size. The EOHIPPUS, of Lower Eocene times, appears to have been not more than eleven inches high at the shoulder, while existing horses measure about sixty-four inches, and the numerous intermediate genera for the most part show regular progress in this respect.

"All these changes have taken place gradually, and a beautiful series of intermediate forms indicating the different stages from Eohippus to the modern horse have been discovered. The sequence of these stages in geological time exactly fits in with the theory that each one has been derived from the one next below it by more perfect adaptation to the conditions of life. Numerous

genera have been described, but it is not necessary to mention more than a few."

The first indisputably horselike animal appears to have been Hyracotherium, of the Lower Eocene of Europe. Another Lower Eocene form is Eohippus, which lived in North America, probably having migrated across from Asia by the Alaskan land connection that then existed. In Eohippus the forefoot had four well-developed hoofed digits and a "thumb" reduced to a rudiment. In the hind foot the great toe had entirely disappeared and the little toe is represented by a splint-bone vestige. Then came Orohippus of the Upper Eocene, Mesohippus of the Oligocene, Protohippus of the Miocene, Pliohippus of the Upper Pliocene, and finally Equus of the Quaternary and Recent. This history, in so far as it concerns changes in the feet and in the teeth, is well shown in the accompanying illustration (Fig. 265). Palæontological evidence of this sort is difficult to controvert. We are not only convinced that the modern horse has descended from a tiny five-toed ancestor, but we can actually read the story of evolutionary progress step by step. And, what is even more important, the horse pedigree is essentially duplicated by that of many others, some of them adjudged by experts to be even more complete.

F. Evidences from Geographic Distribution

1. *General Discussion*

Just as Palæontology may be spoken of as the vertical distribution or distribution in time of organisms, so Geographic Distribution may be referred to as a study of the horizontal distribution of organisms upon the earth's surface at various periods of time. Geographic distribution represents a sort of cross section of vertical distribution, giving a "still" picture of the complex evolution of organisms at one moment of geologic time. The student of geographic distribution is chiefly, but not solely, concerned with the present situation. The study is carried on by explorers and collectors, whose materials are worked over and classified by specialists in the various groups concerned. A map showing the irregular and overlapping ranges of all the species in any one area would be the most complicated picture-puzzle imaginable, and it would be a task of gigantic proportions to make sense out of it. At first thought it might be supposed that organisms are distributed ac-

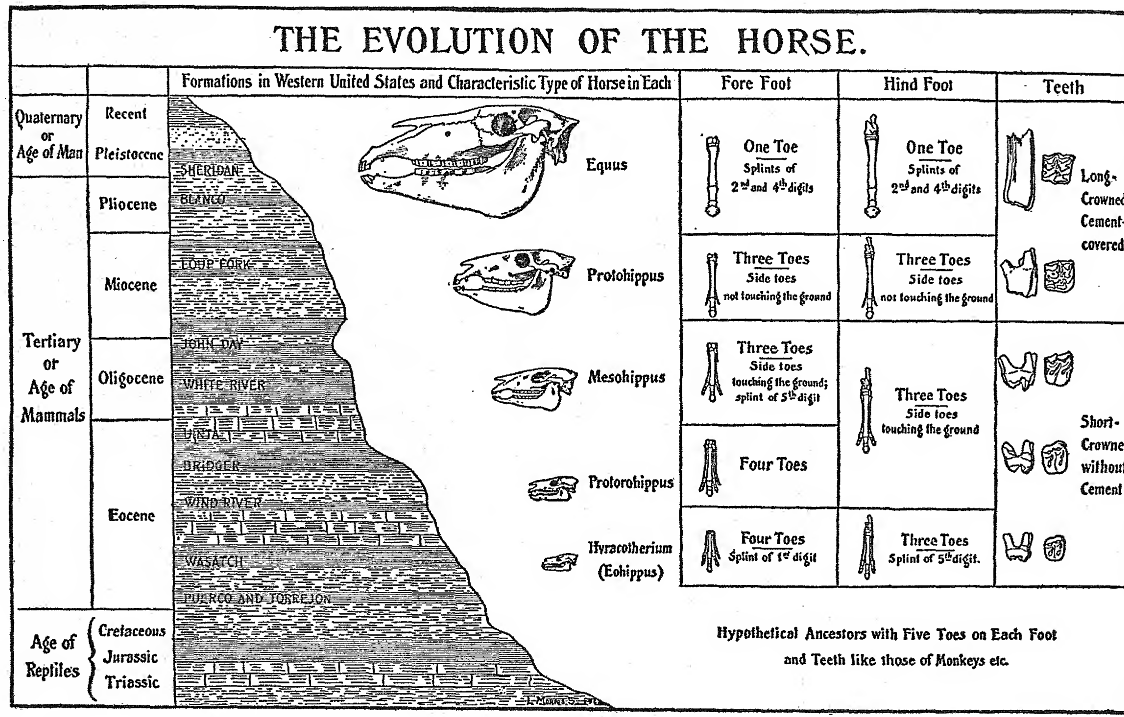


FIG. 265. Graphic presentation of the evolution of the Horse. (From Matthew, 1926.)

cording to climatic conditions or habitat complexes, each species occupying that region of the world best suited to it. A moment's reflection teaches us that this is not at all the case. Essentially similar climatic complexes in different parts of the world have totally different inhabitants; whereas quite similar species commonly occupy very different habitats.

That animals are not always, or even very frequently, found in the best possible habitats is evidenced by the fact that in many instances animals carried far from their native abodes into quite different territory have thriven much better than in the old habitat. The European rabbits, for example, when transported to Australia, throve and multiplied beyond all expectation until they overran the country and became a pest. Again, the English sparrow has found in North America a much more favorable environment than it left behind.

If animals are not distributed according to the plan of having each in the best habitat, how then can we account for their distribution? It is hardly likely that they have always occupied the same ranges they now occupy; for all living things migrate from place to place. The present distribution would be almost totally without meaning were we to confine our attention to it alone: we must study the distributions of the past and thus learn whence the various groups have come. It is only when we study distribution historically that we obtain a clue as to its meaning. Certain facts about the present distribution of species have in themselves a peculiar significance. It seems to be frequently true, for example, that two very closely similar species occupy adjacent ranges and are separated from each other by some natural barrier, such as a body of water or a mountain range. This suggests that one species has been derived from the other and that isolation has kept the derived species from mixing back with the parent species and thus being swamped out by interbreeding. Again, it not infrequently is the case that in a group of species belonging to a single genus the most generalized species occupies the center of generic range and that of the most specialized species are found in the more or less isolated outskirts of the range. Taking these and hosts of other facts into consideration, we seem to have no alternative but to believe that any given species originates in a well defined locality, that it multiplies there and migrates in all available directions, modifying as it goes in accord with various new condi-

tions encountered, and becoming thus split up first into local varieties and, in the course of time, into species. What we have said is a mere paraphrase of the process of evolution, and it thus becomes obvious that the working hypothesis underlying the science of Geographic Distribution is the general principle of descent with modification. The proof that this hypothesis is valid inheres in the fact that, by its use, the whole intricate picture-puzzle presented by the distribution of animals takes on a new significance and becomes intelligible, whereas on any other basis it remains absolutely confusing and meaningless. In other words, the working hypothesis works. It may then be considered valid until proven inadequate to account for the facts, or until a better hypothesis is forthcoming.

If any one phase of geographic distribution may be said to furnish more conclusive evidence of evolution than another, that phase has to do with the peculiar faunas and floras of oceanic islands.

2. *The Inhabitants of Oceanic Islands*

Oceanic islands are small, isolated bodies of land of volcanic origin and located far from continents. They are really no more than the tops of oceanic mountains that appear above the surface of the sea. All such islands have their inhabitants, and a study of these should furnish a crucial test of the rival theories, evolution and special creation. Both evolutionists and creationists agree that these islands have obtained their populations from the continental bodies; for no one has the hardihood to suppose that each tiny island has been the theater of a special creation. If then island species turn out to be exactly like those of the nearest continent, we would be justified in concluding that there has been no evolution of species; but if, on the contrary, the island species turn out to be practically all different from continental species, we would be equally justified in claiming that new species have arisen on the islands. Now the facts are these: Practically all the species inhabiting oceanic islands belong to the faunistic groups of the nearest continent; they consist of types that have the capacity for enduring prolonged transportation through the air during storms or upon floating débris; and the great majority of the species are characterized as "peculiar," i.e., different from species anywhere else in the world. They sometimes belong to the same

genera as those on the continent, but they are at least specifically distinct. The extreme case is that of the island of St. Helena, a very isolated oceanic island 1100 miles from Africa. On this island there live 129 species of beetles, all but one of which are peculiar. These species belong to 39 genera, of which 25 are peculiar. There are also 20 species of land snails, of which 17 are peculiar. Of 26 species of ferns, 17 are members of peculiar genera. St. Helena presents almost a separate small world of species, allied among themselves as though descended from common ancestors, but diverging so far from other known forms as to constitute, for the most part, quite distinct genera.

The Azores, the Bermudas, the Galapagos Islands, the Sandwich Islands, and many others, tell much the same story, but their populations are not quite so peculiar, being for the most part peculiar in species but not in genera—an indication that they are somewhat more recent in origin than St. Helena.

3. *Climatic and Other Ecological Factors in the Distribution of Animals*

In our discussion thus far of the evidences of evolution derived from geographic distribution we have dealt almost exclusively with one type of factor, namely, that involving land and water barriers. There are, however, many other factors, ecologic factors, that are responsible for many peculiar distributions found in animals of today. Every species of animal is adjusted to a definite combination of environmental factors and will be found to be distributed in definite relation to the occurrence of these factors in nature. There may be similar environments far apart from each other and there may be entirely different environments very close to each other, though separated by definite barriers. What is a barrier for one type may be a wide open passage for another.

If we bear in mind these facts we shall find ourselves able to explain some of the odd puzzles of geographic distribution in a manner strictly in accord with the theory of evolution and thus furnish further evidence for evolution. There are, for example, some very strange animal distributions, of which we may mention only a few, that are illuminating for the views just expressed. The polar bears, for example, are found only in the ice covered regions of the north polar region. They should also be found in the south polar regions if animals were created to live in all those

places suited to them. But between the north and south polar regions there is a barrier, impenetrable to polar bears, namely, the hot tropical regions. It seems obvious that the bears as a whole arose in the northern hemisphere and have never invaded the southern hemisphere because they could not stand the heat of the tropics.

Other animals, however, have not been blocked by the tropics. Thus we have an interesting distribution of tapirs, rather primitive ungulates distantly related to horses. These animals are found in two regions both characterized by tropical grass lands and forests, but they are on opposite sides of the globe. One type of tapir is found in South America, another in the tropical Orient. They both are adapted to tropical conditions and there is much evidence that at one time there was a tropical pathway from Asia to North America. Among other things, it is known that coal occurs in the far north, and coal signifies tropical conditions. Tapirs, as is known from their fossil remains, at one time inhabited many regions of Asia and North America where they are now extinct. All of these facts, once they are known, help to clear up the formerly baffling tapir situation.

Many other equally interesting cases of interrupted or otherwise apparently irrational distributions of animal groups have been described and, in each case, the explanation has been forthcoming when the facts have been investigated along lines indicated above. When properly understood, such facts as these, that at first seemed incompatible with the theory of evolution, turn out to afford strong additional evidences in its support.

G. Review of Evidences of Evolution

All the lines of evidence that have been examined, and several others, such as domestication and experimental breeding, point strongly to organic evolution; and none of them are contrary to evolution. Moreover, most of the facts are utterly incompatible with any other theory. Not only do these evidences strongly favor the principle of evolution, but each line of evidence is consistent with all the others, each one helping to make the others more intelligible. Thus, embryology greatly illuminates comparative anatomy; geographic distribution is often greatly aided by palæontology; blood tests aid and are aided by taxonomy. The evolution idea is thus a great unifying and integrating conception that ren-

ders the various branches of biology parts of one coherent science. Any conception that is so far-reaching, so consistent, and that has led to so much advance in our understanding of nature, is at least an extremely valuable idea, and one not to be lightly cast aside in case it fails to agree with anyone's preconceived convictions.

SUMMARY

1. The principle of homology is the basic assumption that underlies most of the evidences of evolution. It is assumed that when two kinds of animals have the same general plan of organization, with the same type of development, this common plan and this common ontogeny has been inherited from a common ancestor.

2. Two structures that have the same relations to other structures in the body plan and develop from the same or similar embryonic primordia are considered as homologous, even if different in appearance and in function. Homologous structures in different groups of animals indicate genetic relationship between them.

3. Many vestigial structures in certain animals are homologous with functional structures in other animals.

4. Analogous structures are those that look alike and function alike, but have a different embryonic origin. They do not indicate genetic relationships.

5. Our system of classification has been based upon homologies. The more completely homologous two groups are, the more closely are they related, and *vice versa*. The use of the principle of homology in classification implies nothing more than an acceptance of the reality of heredity.

6. A phylogenetic tree based on homology and one based on blood tests agree in all essential points. It is quite improbable that two such different criteria of classification would agree unless the resultant arrangement is the only correct one.

7. The evidences from embryology may be interpreted as expressions of the Law of Recapitulation. When critically applied this law throws a great deal of light on ancestral relationships.

8. Good examples of recapitulation are seen in the series of larval stages in the shrimps and in the barnacles.

9. The fossil record is the most direct of the historical evidences of evolution. Fossils speak for themselves and cannot be argued away. They tell a plain story of orderly change in the life of the past.

10. The fossil pedigree of the horse family is one of many convincing chapters in the evolution of higher vertebrates.

11. The horizontal (geographic) distribution of species today would be an unsolvable picture-puzzle were it not studied in the light of evolution. When analyzed as an end product of a long line of geologic and organic evolution, the puzzle clears up and becomes intelligible.

12. One of the strongest evidences of organic evolution comes from a study of the animal inhabitants of oceanic islands. A large proportion

of the species and genera on the islands, though derived from continental ancestors, have so diverged from their ancestors as to be regarded as new species or new genera.

13. The peculiar distributions of polar bears, and of tapirs, are considered as typical of the puzzling situations that are explained in harmony with organic evolution.

14. The strongest feature of the evidences of evolution is that all the various fields of evidence are consistent with each other, throw light upon each other, and supplement each other. None of the facts are incompatible with evolution.

CHAPTER XLVI

GERM PLASM AND SOMATOPLASM

SINCE in all higher animals germ cells constitute the only bridge between two successive generations, it is natural to suspect that much of the mechanism of organic evolution is intimately tied up with the various regular changes involved in the germ cell cycle. It is proposed to study in some detail the nature of germ cells and the changes that go on in them.

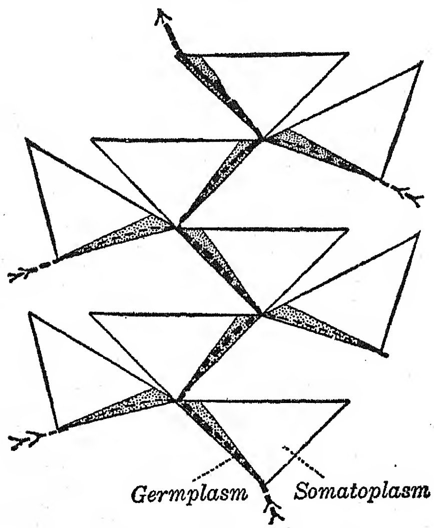


FIG. 266. Scheme to illustrate the continuity of the germ plasm. Each triangle represents an individual composed of *germ plasm* (dotted) and *somatoplasm* (clear). The beginning of the life cycle of each individual is at the apex of the triangle where both germ plasm and somatoplasm are present. In biparental (sexual) reproduction the germ plasms of two individuals become associated in a common stream which is the germ plasm and gives rise to the somatoplasm of the new generation. This continuity is indicated by the heavy broken line and the collateral contributions at each succeeding generation by light broken lines. (From Walter.)

A number of problems arise in this connection, the most important of which are as follows:—What is the relation between the germ plasm and the rest of the organism? At what period in the development of the individual are primordial germ cells first distinguishable? How do gametes arise? What happens to the chromosomes during gamete formation, and what is its evolutionary significance? How are zygotes formed and what is the significance of the process?

A. THE CONTINUITY OF THE GERM PLASM

One of the most extensively discussed theories of modern times is ***Weis-***

mann's theory of the Continuity of the Germ Plasm. According to this theory, a germ cell (zygote) divides by mitosis to form daughter cells that have the same hereditary components as the parent cell. Sometimes very early, sometimes later, some of the cells derived by repeated division of the original zygote become differentiated for various bodily functions and lose their germinal potentialities. Once having become specialized for any bodily function these cells can never form germ cells. There are, however, always left some undifferentiated cells, the primordial germ cells, and these are able to produce new organisms if isolated from the parent body. Thus germ cells produce body cells, but body cells do not produce germ cells; and continuity of type is maintained through an unbroken lineage of germ cells from generation to generation (Fig. 266). Various implications of this theory have given rise to important controversies, especially as to whether the germ cells are entirely insulated from the body so that changes in the body, due to functioning or responses to environmental changes, could have no effect on them. Without attempting at present to discuss this problem, let us examine the facts upon which the Germ-Plasm Theory rests.

If there be an unbroken descent of germ cell from germ cell *ad infinitum*, we should be able to keep track of germ cells from the beginning of one generation to that of the next. This history is known as the germ cell cycle.

B. Periods in the Germ Cell Cycle

The following periods may be more or less arbitrarily marked off in this essentially continuous process:—

1. The fertilized egg or zygote—the beginning of a new individual.

2. The definite segregation or differentiation of one or more PRIMORDIAL GERM CELLS.

3. The early multiplication of primordial germ cells.

4. The rest period, during which there is no mitosis in the primordial germ cells. They merely gather into one or two groups to form the primordia of the gonads (ovaries or testes).

5. The period of multiplication. During this period mitosis is resumed, usually resulting in the production of large numbers of OÖGONIA or SPERMATOGONIA.

6. Some oögonia differentiate into nurse cells and others remain germinal; some spermatogonia differentiate into nutritive or SERTOLI CELLS and others remain spermatogonia.

7. The growth period. During this period there is no further mitosis, but oögonia and spermatogonia grow to form, respectively, primary OÖCYTES and SPERMATOCYTES.

8. The period of maturation, during which the number of chromosomes is reduced to one half that characteristic of the soma of the species.

9. Fertilization, resulting in the production of a zygote with the full number of chromosomes. This is the beginning of another generation.

Some of these periods will now be discussed in further detail.

1. *The Segregation of Primordial Germ Cells*

The exact mode of setting apart of the germ cells is crucial for the Germ-Plasm Theory. There is the widest difference as to the stage of development at which cells may be said to be definitely distinguishable as germ cells. In some cases we can identify germ cells as different from body cells as early as the four-cell stage of cleavage, while in other cases no germ cells can be distinguished as such until a later embryonic or a larval period. The time at which visible segregation of germ cells occurs seems to depend upon how early in embryonic history cellular differentiation of any kind occurs. In many animals the egg, even before cleavage, is definitely organized into regions, and the cytoplasm contains many "organ-forming substances" that are destined to appear only in certain definite blastomeres. These blastomeres, in turn, are set aside for certain definite organs or tissues. The type of cleavage that seems to entail a mere partitioning off of egg regions already differentiated and destined for special organs is known as DETERMINATE CLEAVAGE. There are many other animals, however, in which there is little regional differentiation in eggs at the time of fertilization and in which cell multiplication goes a long way before there is any obvious differentiation of cells. We speak of this kind of cleavage as INDETERMINATE.

In general, it may be said, that in species or groups characterized by determinate cleavage an early segregation of the germ cells may be expected; while in those with indeterminate cleavage a

late segregation is the usual thing. An entirely different way of looking at this problem is to consider all early embryonic cells as germinal and to watch for the first evidences, not of the differentiation of germ cells, but of the differentiation of somatic cells for particular functions. This point of view implies that all cells that have not lost their generalized germinal character by specializing for some particular function or by losing some of the heredity

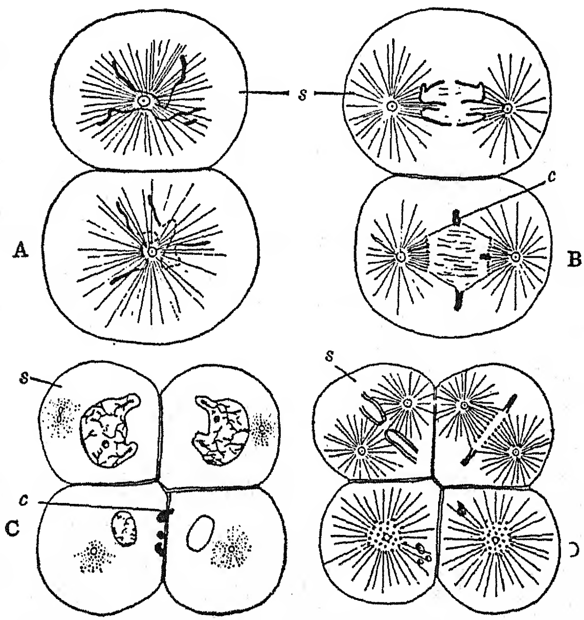


FIG. 267. *Ascaris*. Stages in early cleavage showing the chromatin diminution (*c*) process in all cells except the stem cell (*s*). A, two-cell stage; B, beginning of the four-cell stage; C, four-cell stage; D, beginning to form 8 cells. (From Boveri, 1892.)

material, chromatin, are germ cells. If this view be adopted, it becomes easy to maintain the validity of the continuity-of-the-germ-plasm doctrine, for there could be no break in the lineage of germ cells. Some classic cases that show early segregation of somatic and germinal cells are those of Ascaris and of Miastor.

a. The Case of Ascaris.—*Ascaris megalocephala*, the parasitic mawworm of the horse, has long been a classic object for cytological study. *Boveri,* in 1887, studied and described the early cleavage, especially the early setting aside of the germ cells (Fig. 267).

The first cleavage gives rise to two daughter cells, each with two horseshoe-shaped chromosomes. During the second cleavage one cell divides normally; the other divides in a different way, for each of the two chromosomes breaks up, giving rise to two solid end pieces (*c*) and numerous small granular bits of chromatin derived

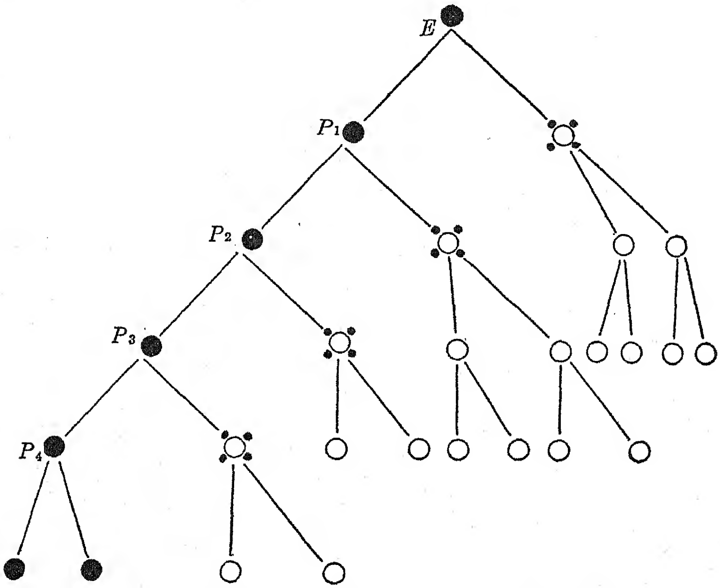


FIG. 268. *Ascaris.* Diagram showing segregation of primordial germ cell. E=egg; P_1, P_2, P_3,=stem (germinal) cells; P_4=primordial germ cell. Circles represent somatic cells, while the four black dots outside of the circles represent the masses of chromatin that are eliminated. (From Boveri, 1910.)

from the middle of the chromosome. The four massive end pieces of chromatin (heredity material) take no active part in the mitotic division and are later resorbed by the cytoplasm; this is known as CHROMATIN DIMINUTION, and the implication is that these cells that have lost some of their heredity material cannot retain the full capacity for producing a new individual, but can give rise only to certain specialized types of organs. As a matter of fact, these first cells to have lost chromatin produce only somatic tissues, while the other two cells that have retained the full complement of chromatin may be looked upon as still germinal. Now, in the next division, passing from the four- to the eight-cell stage, one

of the two "germinal" cells divides normally and the other divides with the accompaniment of chromatin diminution, as before, and the division products of this latter cell are set aside to form somatic tissues. The remaining cell retains all of its chromatin and is therefore still germinal. It, however, divides into two cells, one of which undergoes chromatin diminution and gives rise to somatic tissues; the other remains germinal. This last cell contributes once more to the formation of the soma; after that it divides several times more, giving rise only to germ cells. This history is shown in the accompanying diagram (Fig. 268). It is clear then that in Ascaris there is no break in the continuity of the germ plasm.

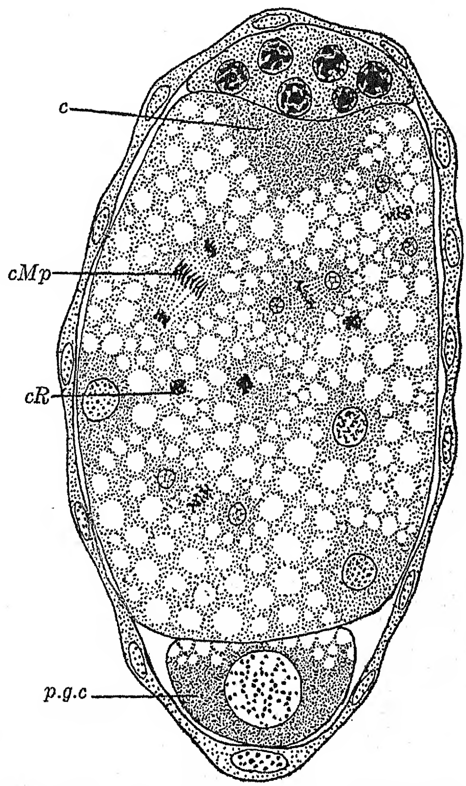


FIG. 269. *Miastor americana.* Longitudinal section of egg with one germ cell (*p.g.c*) and nuclei undergoing chromatin-diminution process. c = cytoplasm; cMp = chromosome middle plate; cR = chromatin remains. (From Hegner.)

b. The Case of Miastor (Fig. 269).—This case is not so very different from that of Ascaris. The egg is rather definitely organized before cleavage begins. At the vegetal pole of the egg there is a mass of material known as POLE PLASM. When the first division of the egg occurs, one daughter nucleus goes into the pole plasm and becomes the first germinal nucleus, destined to give rise by further divisions to all the germ cells of the individual (Fig. 269). The other daughter nucleus divides several times, undergoing chromatin diminution each time and thereby sealing

its fate as a possible mother of germ cells. Many similar cases of early germ cell segregation—perhaps it would be more correct to say early somatic differentiation—have been described in species belonging to most of the large groups of animals.

In the vertebrates the germ cells and body cells cannot be distinguished until relatively late, but the vertebrates are slow to specialize tissues of any sort, and perhaps it would not be incorrect to say that for a long time vertebrate embryonic cells are all essentially germinal. In concluding this phase of the discussion, it may be said that in higher animals there is probably an absolute distinction between germ cells and somatic cells in some groups of animals, but that in some of the lower animals the distinction is not a rigid one, and that in such animals there is always the possibility that certain unspecialized somatic cells may take on a germinal function when the conditions demand.

2. *The Period of Multiplication*

Soon after the primordial germ cells aggregate to form the early gonads a period of multiplication ensues, which results in the dividing cells becoming smaller and smaller as they become more numerous, because very little growth takes place between mitotic divisions. In Miastor (Fig. 270, lower half) this period results in the formation of sixty-four oögonia. In several other species the number is equally limited and exactly known.

3. *The Period of Growth*

Growth of the oögonia and spermatogonia takes place more or less at the expense of some of the potential germ cells that give up their germinal function and become nurses and feeders to the cells destined to be mature germ cells. Thus a few cells are enabled to grow large and well fed at the expense of a good many others. One very important event occurs during the growth period: homologous chromosomes come together in pairs—the phenomenon known as SYNAPSIS. This event seems to look forward to reduction in the number of chromosomes to one half the somatic number, thus making it feasible for the male and female gametes to unite without increasing the specific number of chromosomes.

4. *The Period of Maturation*

The process of maturation (Fig. 271) involves two divisions of the germ cells that differ entirely from any others in that in one of

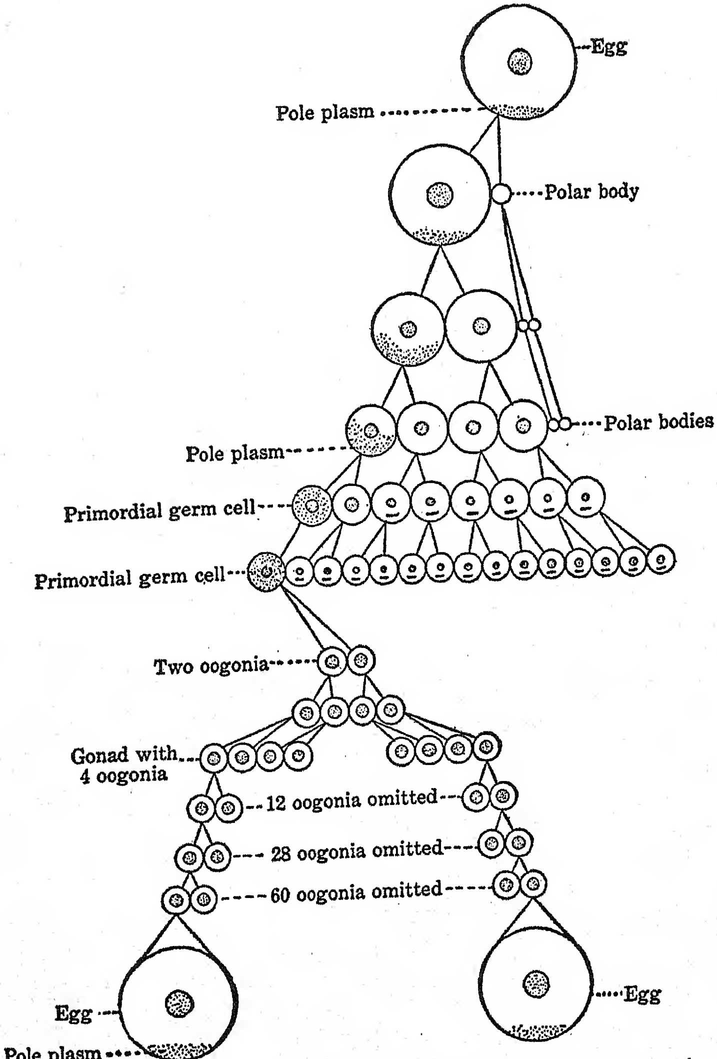


FIG. 270. *Miastor americana.* Diagram illustrating origin and history of germ cells from one generation to the next. (From Hegner.)

these divisions whole chromosomes, instead of half chromosomes, go to the two daughter cells. More specifically, the paired homologous chromosomes that had united during synapsis separate and go to different daughter cells. This means that homologous maternal and paternal chromosomes contributed by the parents always go to different gametes. Now since the distribution of the maternal and paternal components of one pair of chromosomes is quite independent of that of all other pairs of chromosomes, there is possible a very wide range of diversity in the shuffling and dealing of the hereditary characters of the germ cells. The second maturation division is somewhat of a puzzle. It does not affect the distribution of the hereditary units, but it does allow chromosomes, already split lengthwise during the first maturation division, to become properly distributed to daughter cells. This is necessary if the number of chromosomes in the gametes is to be reduced to one half in preparation for the union of gametes into zygotes. The maturation mechanism is believed to be one of the most important factors involved in evolution, for it gives rise to a tremendous variety of combinations of maternal and paternal characters.

5. *The Formation of Zygotes* (*Fertilization*)

From the evolutionary standpoint the chief effect of the union of gametes to form zygotes (Fig. 271, **F**, **G**) is the production of a great variety of combinations of different assortments of hereditary units of two different stocks. This makes it possible for the most favorable characters of different stocks to become united in a single individual. The evolutionary significance of this can scarcely be overemphasized.

C. The Germ-Plasm Theory Criticized

There are at the present time many zoölogists, especially those who have a physiological bent, who abhor the idea of the separateness or apartness of the germ plasm. They look upon the organism as a unit, each part of which is integrated with all others. In view of all of the coördinating systems with which the higher organisms are endowed, it seems to them inconceivable that one part of an organism could be physiologically isolated from all the rest. Objection is also raised to the doctrine that germ cells are always derived from previously existing germ cells in an unbroken line of

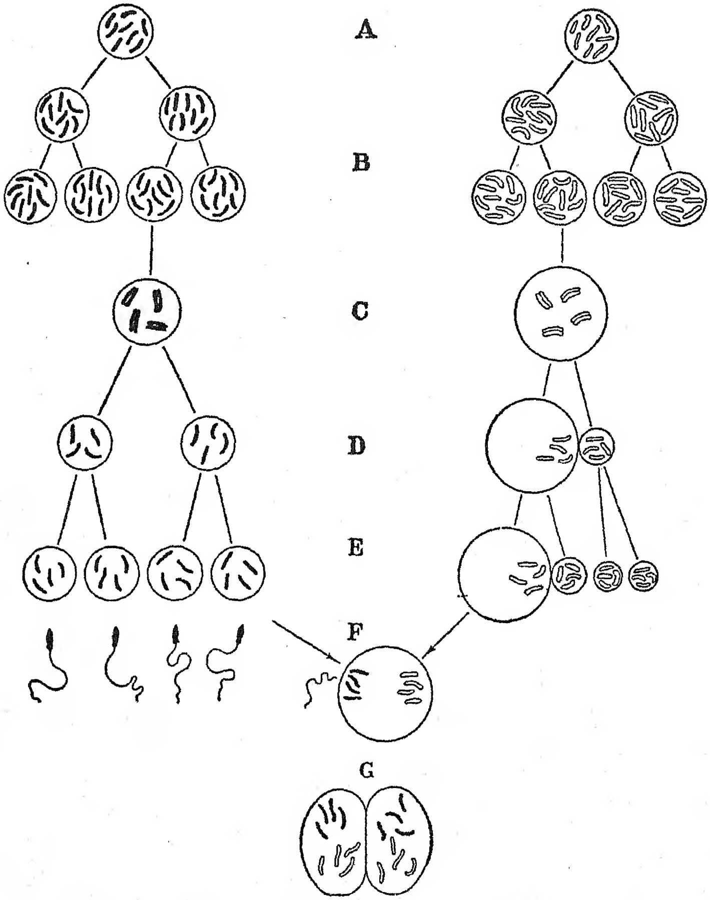


FIG. 271. Diagram of the general plan of spermatogenesis and oögenesis in animals. The somatic, or diploid, number of chromosomes (duplex group) is assumed to be eight. Male, to the left; female, to the right. A, primordial germ cells; B, spermatogonia and oögonia, many of which arise during the period of multiplication; C, primary spermatocyte and oöcyte, after the growth period with chromosomes in synapsis; D, secondary spermatocytes and oöcytes, with haploid number (simplex group) of chromosomes, which have arisen by the first maturation (reduction) division; E, spermatids (which become transformed into sperm) and egg and three polar bodies which have arisen by the second maturation (equation) division; F, union of sperm and egg (fertilization) to form zygote with diploid number (duplex group) of chromosomes; G, chromosome complex of cells after first division of the zygote, and of all subsequent somatic cells, and germ cells until maturation. (From Woodruff.)

germinal antecedents; for the claim is made that in many animals, and especially in some vertebrates, the primordial germ cells disintegrate during larval life and new germ cells are differentiated out of epithelial cells—cells that have always been classed as somatic. Even if functional germ cells in certain cases are derived from epithelium and not from primordial germ cells, there is involved no genuine break in germinal continuity, for even epithelial cells are linear descendants of the original zygote. The only question at issue is whether epithelial tissues are to be considered as having become specialized for a particular function; whether, in other words, we are justified in calling them somatic tissues rather than reserve germinal tissues. The second alternative seems more reasonable.

SUMMARY

1. The main problem raised and discussed in this chapter is that of the origin of germ cells. The crucial point is whether germ cells are derived from transformed body cells or are derived by mitosis from an unbroken ancestry of germ cells.

2. Weismann's theory of the Continuity of the Germ Plasm is discussed and illustrated. This theory is a fundamental postulate of modern genetics.

3. The various periods in the germ cell cycle are listed and described.

4. The question as to just when the germ cells are set apart from body (somatic) cells should probably be stated in reverse fashion: when are the body cells first set apart from germ cells? The time in the development of the individual when the first differentiation of body cells and germ cells is evident varies greatly in different groups. Ascaris and Miastor show very early differentiation of somatic and germ cells, while vertebrates and echinoderms show relatively late differentiation of recognizable germ cells, but there is evidence that germ cells are present throughout ontogeny.

5. The most significant phase in the maturation of germ cells is that in which homologous pairs of chromosomes come together in synapsis and then one of each pair goes to a separate cell, the gamete. Gametes have the haploid number of chromosomes, consisting of one chromosome of each pair.

6. In fertilization two gametes (egg and sperm) fuse to form a combination cell, the zygote, which has the diploid number of chromosomes, two of each kind.

CHAPTER XLVII

SEX AS AN EVOLUTIONARY MECHANISM

A. The Phenomena of Sex Outlined

a. Sex Defined.—It is not easy to give an adequate definition of sex. Dictionaries define it as "the distinguishing peculiarity of male and female"; as "either of the two divisions of organic beings distinguished as male and female." These definitions really evade the issue, but it is very difficult to offer a suitable substitute. We can get at a definition in a somewhat round-about way by saying that sex comprises that whole set of phenomena that center about gametic reproduction. Any individual, then, is sexual if it produces gametes—ova or spermatozoa, or their equivalents. Thus we would be justified in calling any individual that produces ova a female, and one that produces spermatozoa a male. One that produces both kinds of gametes is a male-female or, more technically, a HERMAPHRODITE. Thus we may say that the PRIMARY SEXUAL CHARACTERS of individuals are the ova or the spermatozoa, and that maleness or femaleness is determined by the possession of one or other of these two types of gametes.

b. Secondary Sexual Characters.—There are usually, especially in higher animals, many differences between males and females in addition to the possession of eggs or sperms. The two sexes may differ in size, in form, in coloration, in the accessory organs of reproduction, in instincts and behavior, in adaptations for feeding and taking care of young. While some of the lower animals differ visibly only in their primary sex characters, the general rule is a more or less pronounced SEX DIMORPHISM. An extreme case of this phenomenon is that of one of the scale insects, *Aulocaspis rosæ* (Fig. 272), in which the adult male is a fairly typical insect with wings, antennæ, and legs, but has no mouth; while the adult female has no legs, wings, or antennæ, but has a mouth.

c. Sex as an Adaptation.—In discussing any biological phenomenon, one question inevitably comes to be asked: What is the advantage of it or in what way is it of value to the species possessing it? In previous chapters we have had occasion to point out

some of the ways in which sex appears to be of value. It is obvious that sex is an important agency in promoting reproduction; but it should not be forgotten that in very many instances reproduction is carried on successfully without the intervention of mating

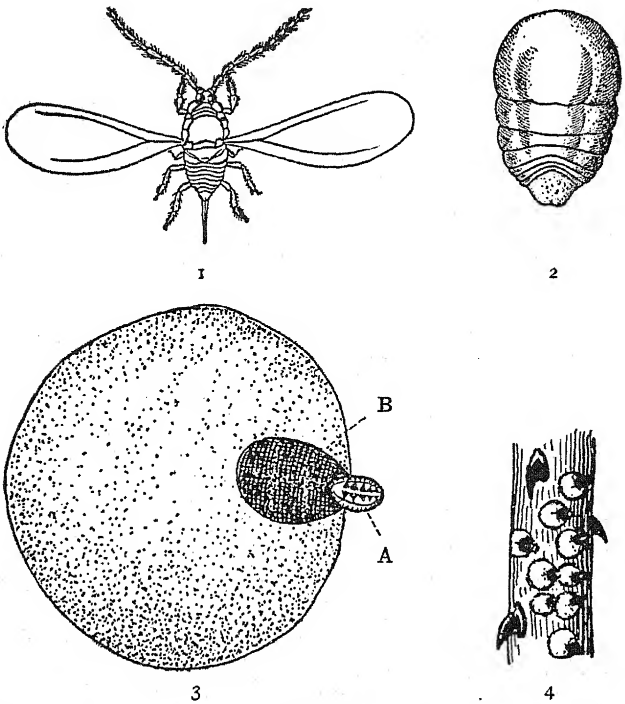


FIG. 272. The rose scale (*Aulocaspis rosæ*), an extreme case of sexual dimorphism. 1, Adult male, with 2 wings, 2 antennæ, 6 legs, but no mouth. 2, Adult female; legs, antennæ, and wings not developed, but mouth (on under side) well developed. This female never leaves the scale (3). The scale shows the cast skin of the larva at A, the second cast skin at B, and the white adult scale covering the female. 4 shows the scales on a rose branch, twice natural size. (Drawings by R. Weber, from Cockerel's "Zoölogy" World Book Co.)

or true sexual congress. Among the higher organisms, however, sexual dimorphism accompanied by sexual congress is practically universal. The more highly specialized organisms are in other respects, the more pronounced sexual dimorphism they are likely to display. Thus sexual dimorphism is merely one phase of specialization. Just as it is a better scheme to have certain cells or

tissues performing but one function apiece and doing the job expertly, so it is in the interests of increased efficiency to have the two sexes as highly specialized and differentiated from each other as possible, so long as the characters in which they differ are of value.

We can readily understand that sex in its more advanced and highly perfected states is a reproductive adaptation of great consequence, but what can be said of the value of the simplest expressions of the sexual phenomenon that consist of nothing more than a union of apparently similar gametes? A ready answer to this question might be that whenever gametes unite they bring together germ plasms that differ in certain respects and that such combinations may be more favorable than either of the uncombined conditions. In the higher animals it is clear that, during the maturation divisions, a sort of shuffling and dealing of maternal and paternal genes—the determiners of adult characters—takes place, and this results in a great variety of different combinations of the parental genes, a different combination being distributed to each gamete. This being true, whenever any two gametes unite to form a zygote, a unique individual is likely to be produced; for it is very unlikely that, with so many different combinations possible in different gametes, the same kind of sperm and egg would ever chance to come together more than once. Thus it seems certain that sex is an agency capable of producing almost infinite diversity among the individuals of a species, and out of a very wide range of individuals differing in a great many ways there will obviously be some that are better adapted to the conditions of life than others. This forms the basis for Natural Selection, or the survival of the fittest, believed to be an important factor in progressive evolution. Sexual reproduction then may be looked upon as a mechanism that is continually grinding out new forms that have to run the gauntlet of selection.

B. The Determination of Sex

a. Early Theories.—What is it that settles whether a given zygote, or fertilized egg, shall give rise to a male or a female? This is an old problem, and many theories have been advanced to explain it. ***Hippocrates*** long ago guessed that the sex of any offspring depended upon the relative vigor of the two parents, the stronger of the parents impressing his or her sex upon the child.

This theory fails to account for the fact that in many animals that give birth to several young at a time there are both males and females in the litter. Several authors have claimed that sex depends on the relative ripeness or staleness of the gametes at the time of fertilization. Another theory, widely accepted for some time, was that the condition of nutrition of the mother during pregnancy, or during the growth period of the eggs, determined the sex: that a well nourished mother tended to produce females and a poorly nourished mother, males. Some color was lent to this hypothesis by the fact—if it is a fact—that there is an increased ratio of male to female births in the human species during and immediately after periods of war and of famine, when conditions of nutrition are bad.

b. Sex Determined at the Time of Fertilization.—Evidence has been steadily accumulating within the past twenty years or more that sex is determined definitely, and in some cases irrevocably, when the egg is fertilized by the sperm; that the particular combination of chromosomes that is brought together when the gametes unite settles the sex. Perhaps the most positive proof of this, apart from cytological examination of the germ cells themselves, comes from a study of the reproduction of the nine-banded armadillo. This interesting mammal has the specific peculiarity of always—the exceptions are almost negligible—producing four offspring at a litter (Fig. 252). Invariably all the members of a set of quadruplets are of the same sex and are nearly identical in their other bodily characters. The explanation of this is that in every case a set of quadruplets is derived from one zygote that divides at an early embryonic period into four separate embryos. The sex must have been decided before the four embryos separated, and it never changes afterwards. Moreover, the separation of embryonic rudiments occurs so early that the presumption is that the sex was already determined at the time of fertilization. Other cases of the same sort are those seen in some of the parasitic hymenoptera and in human identical twins. In some parasitic hymenoptera the eggs are laid in the eggs of butterflies by the wasplike mother, and at an early embryonic stage the embryo parasite divides into hundreds of separate embryonic parts, each of which produces a complete grublike larva parasitic in the body of the larva of the butterfly. Each grub produces an adult, and all individuals derived from one egg are of the same sex. Human identical twins are also either

both males or both females, and there is every reason to believe that they are the product of the division of a single egg in each case; yet this has never been absolutely demonstrated as it has in the case of the armadillo.

C. The Chromosomal Mechanism of Sex Determination

a. Chromosomal Mechanism as Exemplified by Drosophila.— When geneticists first came to realize the importance of the chromosomal mechanism of heredity, it was natural enough for them to look for sex differences in the chromosomes. Investigation showed that the cells of the males and of the females in many species of animals differ in the number, size, or shapes of chromosomes. Moreover, there were usually some of the chromosomes that showed sex differences while all of the others were alike in both sexes. This difference in chromosomes according to sex is well illustrated by the germ cells of the classic fruit fly, *Drosophila melanogaster* (Fig. 273), which has furnished so much valuable data to genetics. The cells of the female possess eight chromosomes, two of each of four kinds. There are two pairs of rather large bent chromosomes, one pair of minute spherical chromosomes, and one pair of straight rodlike chromosomes—the latter shown in black in the figure. The first three pairs mentioned are known as AUTOSOMES and are the same in both sexes. The pair of straight chromosomes, shown in black, are known as the X-CHROMOSOMES and are believed to play an important rôle in sex determination. When we examine the male germ cells, we find that the only difference to be noted is in connection with the X-chromosomes, for, instead of two straight X-chromosomes, as in the female, the male cells possess one X-chromosome and one hook-shaped chromosome of about the same size, known as the Y-CHROMOSOME. A female Drosophila has the chromosomal combination XX, while the male has the combination XY. All of the body cells have the same chromosomal condition as have the germ cells of the same individual. So far, we have only succeeded in describing only another type of sex dimorphism, but we fortunately have been able to discover the mechanism by means of which this dimorphism and its consequences have been brought about. The accompanying diagram (Fig. 273) shows the maturation divisions leading to the formation of both eggs and spermatozoa. Note that, in the case of the egg, when the numerical reduction

of chromosomes has taken place, each gamete has an X-chromosome. In the case of the sperm, however, the gametes are of two kinds, one having an X-chromosome and the other a Y-chromo-

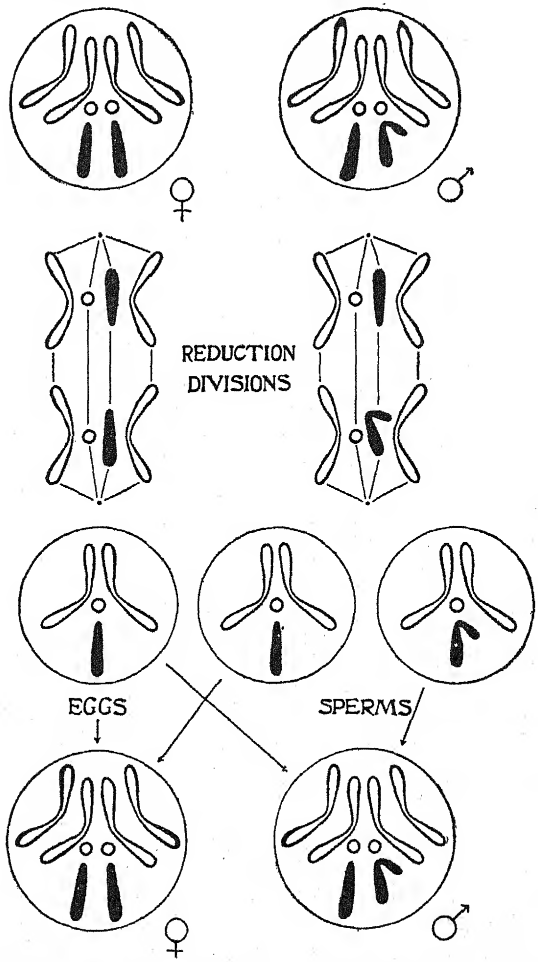


FIG. 273. Diagram to show chromosome relations in the inheritance of sex in *Drosophila melanogaster*. (From Babcock and Clausen.)

some. Thus two kinds of sperms are produced in equal numbers and each kind has an equal chance to fertilize eggs. The result is that half of the eggs are fertilized by X-sperms and half by Y-sperms. When an X-sperm fertilizes an egg, the result will

always be an XX-zygote, which is a female; but when a Y-sperm fertilizes an egg, the result will always be an XY-zygote, a male. Thus we have in the process of maturation and fertilization a mechanism not only for producing males and females, but one for maintaining a 50:50 ratio between the sexes.

Until quite recently it has been supposed that the X- and Y-chromosomes carried special determiners for sex, but ***Bridges*** has demonstrated that it is not so simple a matter. According to this keen investigator, the important factor is the balance, more or less quantitative in character, between the X-chromosomes and the rest of the chromosomes (AUTOSOMES). It appears that X-chromosomes carry genes for femaleness and autosomes those for maleness. Thus all zygotes are equal for maleness, but they differ in femaleness. Two X-chromosomes, which are female in their tendencies, are sufficient to overbalance the six autosomes in the female direction; but if only one X-chromosome is present, it is insufficient to overbalance the autosomes, and the male condition prevails, for the combined tendency of the autosomes is toward maleness. In certain exceptional cases Bridges found that, as the result of a slip in the maturation mechanism, some few eggs were produced with extra autosomes. When such eggs were fertilized by sperms carrying the X-chromosomes, zygotes were produced with two X-chromosomes and seven or eight autosomes instead of the usual six. Individuals developing from such zygotes were not normal females, even though they had the XX combination, but were INTERSEXES, showing all sorts of conditions intermediate between those of regular males and females. In others an additional X-chromosome was shown to swing the balance beyond the typical female condition. The Y-chromosome appears to be negative so far as sex determination is concerned, but Bridges has shown that in certain rare cases where zygotes had been formed without a Y-chromosome, male individuals, apparently normal in other respects, were produced, but they were always quite sterile. Certain other revelations as to the chromosomal mechanism of sex determination have come to light, but the above analysis has proceeded far enough for our purposes.

The question now arises as to whether the mechanism which seems to have been definitely demonstrated in Drosophila is paralleled in other animals. With various modifications as to details, it seems to be true that some such mechanism as that de-

scribed is responsible for sex determination in at least the vast majority of animals and in not a few plants. Man, for example, has 48 chromosomes, with two X-chromosomes in the female and an X- and a Y-chromosome in the male.

b. Sex Determination in Moths.—In moths the mechanism just described for Drosophila is just reversed, in that the males have the XX condition and the females the XY condition. Thus two kinds of eggs are produced and only one kind of sperm. Apart from this shifting of the chromosome condition between the two sexes everything else works out essentially as in Drosophila.

c. Sex Determination in Parthenogenetic Species.—Even in those well-known cases where development takes place without fertilization, the facts are consistent with the above analysis of the mechanism of sex determination. In the bees, for example, all fertilized eggs produce females—either fertile queens or infertile workers—and all unfertilized eggs produce males, known as drones. Cytological examination shows that all eggs undergo maturation and that each egg possesses one X-chromosome. All functional spermatozoa, for reasons that will presently be explained, also possess one X-chromosome. The result is that all eggs that are fertilized receive an X-chromosome from each gamete, giving the XX combination, and therefore produce females; while all eggs that pass out of the oviduct without fertilization have the reduced number of chromosomes, including but one X-chromosome, and therefore produce males. Two points need further elucidation. One is this: If sex determination depends on the balance between the X-chromosomes and the autosomes, why is it that in the bees two X-chromosomes and the diploid number of autosomes give the female condition, while one X-chromosome and the haploid number of autosomes give the male condition? Obviously the balance between autosomes and X-chromosomes is exactly the same in both sexes. From this it would appear more logical to assume, as has usually been done, that in this group of animals the autosomes have little to do with sex determination and the one X-chromosome by itself determines maleness and the two X-chromosomes, femaleness. The other point still unexplained is this: Why is it that, in the bees and wasps, all functional spermatozoa have the same chromosome complex—that with one X-chromosome? Let us remember that males have the reduced number of chromosomes from the start,

and that, therefore, they cannot very well undergo further chromosomal reduction. So strong is the force of heredity, however, that the male spermatocytes go through the motions of undergoing maturation, but omit the essential feature of this process, the reduction division. When the first maturation mitosis takes place, all the chromosomes go to one pole and a very unequal cell division takes place, resulting in one large spermatocyte of the second order possessing the normal haploid number of chromosomes and a small abortive spermatocyte without any nucleus, which of course is incapable of life. Hence each functional spermatozoön possesses the normal haploid number of chromosomes with one X-chromosome. Since all female gametes and all functional male gametes carry one X-chromosome, each fertilized egg has the two-X condition and will be genetically a female; which is actually the case.

In other parthenogenetic groups, such as the aphids, parthenogenetic eggs for several generations produce only females. Later in the season, however, a generation of males and females is produced parthenogenetically. The problem is to account for the origin of the males. It has been found that at a definite point of the germ cell cycle some of the germ cells have extruded an X-chromosome, thus giving rise to the male condition. The males and females of this generation mate and produce winter zygotes capable of living through the winter and developing the following spring. When they develop they form exclusively females, stem mothers, that start off the series of parthenogenetic generations. The reason why only females are produced as the result of the mating of males and females is that only one kind of spermatozoön is viable, the one lacking an X-chromosome never living long enough to be functional.

D. Concluding Remarks

It now seems clear that not only are the mechanisms of gamete formation and of the union of gametes to form zygotes important factors in evolution, but equally important are the mechanisms by means of which male and female individuals are produced. In some of the higher animals, especially the vertebrates, it has been shown that the chromosome mechanism alone is inadequate to complete the job of producing full-fledged males and females. In our discussion of various physiological processes controlled by

hormones we have already brought out the fact that in vertebrates the complete differentiation of secondary sexual characters depends upon sex hormones secreted by the glandular parts of ovaries and testes. The difference between the two situations seems to be as follows: In the arthropods all the cells of the body retain the capacity to produce either male or female differentiating substances, while in the vertebrates this function becomes delegated to certain specialized cells, the endocrine glands of the gonads, and other body cells lose that capacity. It seems highly probable, moreover, that the sex-differentiating substances are of the same character (are hormones) whether produced in all cells or only in certain specialized cells.

It may be stated in concluding this account of sex as an evolutionary mechanism, that we have shown that the chromosomes have a very definite rôle in the determination of sex. It will soon become equally obvious that chromosomes are equally important in variation and heredity in general. In the next chapter the Chromosome Theory will be expounded in some detail.

SUMMARY

1. Sex is a term applied to those phenomena that are associated with gametic reproduction. Primary sex differences are those that distinguish individuals producing eggs (females) from those producing sperms (males).
2. All somatic differences between males and females are called secondary sexual characters. When males and females differ markedly in their somatic characters they are said to exhibit sex dimorphism.
3. The main function of sex is that of increasing variability. This is accomplished by uniting in one individual an assortment of the peculiar hereditary characters of two individuals, the parents. Sex is less effective as a pure reproductive mechanism than is spore reproduction or various kinds of asexual reproduction.
4. Sex is determined, as a rule, by a chromosomal mechanism, which is described in detail for Drosophila. This same mechanism is found in most animals, including man.
5. Various modifications of this typical sex-determining mechanism are described. They are all compatible with the Chromosomal Theory.
6. Environmental changes may, and do sometimes, change the outcome of sex differentiation. In some cases an individual that was chromosomally determined to be a female is changed into a male, and *vice versa.*

CHAPTER XLVIII

CAUSAL FACTORS OF ORGANIC EVOLUTION

A. The Facts of Evolution versus the Mechanism of Evolution

That animals and plants arose many millions of years ago, that they were at first relatively small and simple and have gradually become more and more specialized and diversified, that modern forms are the present end products of a long series of more or less orderly changes, and that evolution is still actively going on, may now be regarded as facts that are supported by adequate evidences, some of which have already been presented.

We not only have evidence as to the actuality of the evolutionary processes in general, but in many instances we have been able to discover the detailed course that evolution has followed in certain particularly favorable animal and plant stocks. Thus in the very fine fossil pedigree of the horse family and many other equally adequate fossil series we have displayed before us not only the general fact that certain present-day specialized types have descended from ancient more generalized ancestors, but we have much detailed information as to the actual course of their evolution.

That evolution has taken place and that it has followed certain definite progressive trends are now regarded as established facts. It is, however, one thing to know the facts about a process and quite another thing to understand the causes and mechanisms underlying that process. It is our purpose in the last part of this volume to present something of what we know about the actual causal factors of evolution, the mechanisms of racial change and adjustment.

B. The Five Main Causal Factors of Evolution

Biologists generally agree that the mechanism of organic evolution is an extremely complex one and that the course of evolution is influenced by a great many factors, some of which are regarded as of major significance and others as of relatively minor impor-

tance. While there is a good deal of disagreement as to the relative importance of these factors there is little question as to the high importance of at least five major factors which may be listed as follows:

1. The Persistence Factor (Heredity)
2. The Diversity-increasing Factor (Sex)
3. The Change Factor (Mutation)
4. The Guiding Factor (Selection)
5. The Dividing Factor (Isolation)

C. The Interdependence of Evolutionary Factors

None of these factors operates alone, but all work together like the closely meshed parts of a complex machine. Each factor influences the operations of all the others and is itself influenced by them. Hence we have an interlocking system of causal factors of organic evolution.

Thus, if the persistence factor, heredity, had operated alone and had worked without slips, the original form or forms of life units would have persisted unchanged and the world of life would have long ago come to an evolutionary standstill. If the change factor, mutation, had operated alone, without heredity, the organic world would be a chaos and no two generations would be at all alike. With both heredity and mutation, but no guiding factor such as selection, the world would now be peopled with monstrous and ill-adapted creatures. With heredity, mutation, and selection operating normally, but without sex and its mechanisms for enhancing diversity, the processes of evolution would have proceeded at a much slower pace than they have. With all of the other four factors operating normally, but without some sort of effective isolation of parts of a species from the main species population, there could have arisen only one or a few adaptive types instead of the multiplicity of different types that actually exists. While heredity and mutation are commonly regarded as the primary factors of evolution, the other three are now regarded as indispensable participants in the process.

It is our purpose in this course to deal rather extensively with the first three factors (the persistence, the diversity, and the change factors) and to give only scant attention to the guiding and dividing factors. The reasons for this procedure will be obvious to biologists: the first three factors are relatively well understood and

their mechanisms can be readily made intelligible to beginners, while the last two factors are less completely understood and there is still a good deal of controversy as to the ways in which they operate and the extent to which they may be regarded as indispensable factors.

The persistence, the diversity, and the change factors constitute the main subject matter of that branch of biology known as GENETICS, one of the most progressive of the modern subsciences of biology. These three factors are so intertwined that it is almost impossible to study one without the others. As a matter of fact the diversity factor has long been regarded as an integral feature of heredity, for pure heredity apparently is nearly always upset by the other mechanisms. What are known as Mendel's Laws of Heredity are primarily the laws governing diversity. Mutation is also not independent of heredity, for in a sense mutations may be regarded as disturbances or irregularities in heredity. Moreover, mutations could never have been discovered until a rather complete knowledge of heredity and its accompanying diversity had been attained. Because of this intimate interrelationship of the three primary factors of evolution, it is customary to study them together and we shall proceed to do this without trying to draw any very sharp lines of distinction between them.

D. The Relation of Genetics to Subjects Already Discussed

Before we begin our discussion of the operation of the heredity mechanisms it may be well to remind you that we have already presented many facts pertaining to these subjects in preceding chapters. Thus in dealing with classification as based on homologies we have assumed the validity of heredity. In the chapter on modes of reproduction we have dealt with the ways in which specific characteristics of parents are passed on to offspring, which of course is a matter of heredity. In the discussion of sex and its implications we have dealt with certain aspects of the diversity mechanisms. And in the chapter on the Germ-cell Cycle we have dealt with the Continuity-of-the-Germ-Plasm as the chief mechanism of persistence of type, and with the maturation and fertilization processes of germ cells, which constitute the chief mechanisms of diversity. We also introduced quite early in the book a study of Mitotic Cell Division, a mechanism that is probably more im-

portant than any other factor in the persistence of type from generation to generation. While, therefore, the subjects now to be studied are not at all new, there are certain entirely new aspects of heredity and diversity that have as yet remained untouched and constitute some of the most striking features of modern biology.

This chapter is so nearly a summary in itself that a formal summary is omitted.

CHAPTER XLIX

HEREDITY AND VARIATION

A. Heredity without Genetic Variation

Since sexual (gametic) reproduction has been assigned the evolutionary rôle of increasing the diversity of races, it is fairly obvious that, for the study of heredity proper, we must choose as materials certain types of animals and plants in which gametic reproduction is either absent or is at least not operating as a diversity-increasing mechanism. We find in a great many kinds of organisms the set-up necessary for such studies of pure heredity, disturbed only by the operation of the mutation mechanism, a factor that in ordinary short-time breeding experiments may be ignored.

Out of a multiplicity of modes of reproduction in which heredity proper may be studied to advantage we shall discuss only four: 1, vegetative propagation; 2, fission and budding; 3, parthenogenesis; 4, twinning.

1. *Vegetative Propagation*

Every one knows that certain plants are commonly propagated by means of cuttings. A small portion of a plant, such as a piece of branch or even a single leaf, may be removed and, if planted in suitable soil, will take root and develop into a new plant. A potato tuber is an enlarged portion of an underground stem, which if planted will grow into a whole potato plant. Some plants propagate themselves in nature in this way. Thus a strawberry plant sends out runners, long stems, which take root at intervals and give rise to new plants at some distance from the parent plant.

In all cases of this sort the new individuals are merely extensions of the body (soma) of the parent plant. Since, therefore, the soma of an individual consists of cells that are all alike in their hereditary materials, no matter how extensive may be the growth of that soma, all parts must be genetically identical.

Why then are there differences among the progeny of a given individual produced by vegetative propagation? Differences in size and vigor are due to differences in the environment. Thus one

shoot cut off from a given plant may produce a large and vigorous plant if placed in good soil and kept under other favorable conditions, while another shoot from the same plant may produce a stunted and sickly plant if planted in poor soil and reared under unfavorable conditions. Such variations as these are not inherited, as can be shown if one takes a shoot from the stunted plant and another from the well-grown plant and rears them both side by side in good soil. After a time they will produce plants of equal quality. Thus we see that somatic changes which are the result of environmental differences are only temporary and restricted to one generation. Such changes are known as *somatic modifications* and have not as yet been shown to be hereditary. You will have occasion to recall these statements when we come to discuss Lamarck's theory in the next chapter.

In plants reproducing vegetatively, and in that way alone, the only chance for evolution to take place would be through changing the hereditary material in one or more cells. Such changes actually occur occasionally and are known as SOMATIC MUTATIONS. Now and then a single branch of a tree is seen to have a different type of leaf or fruit from those in the rest of the tree. If one wishes to perpetuate the new conditions one resorts to grafting pieces of this mutated branch on the trunks of other trees. Navel oranges and certain varieties of apples are propagated in this way.

2. *Fission and Budding*

The entire progeny of a single Paramecium derived from repeated divisions of the individuals constitute what is known as a CLONE, a group of offspring produced without sexual reproduction from a single parent individual. A clone of this sort is easy to rear. One has merely to isolate a single Paramecium in a culture dish and let it multiply. In the course of a couple of days there will be thousands of offspring. (Of course, when conjugation occurs the continuity of a single hereditary complex will be broken up, but this is because sexual reproduction has intervened.)

Jennings has studied variation and heredity in clones of Paramecium and reports that there is a great deal of variation among the members of a given clone, but that the differences among individuals are not hereditary. For example, it is a simple matter to isolate the largest member of a given clone into one culture dish and the smallest into another. After a day or so each will have

produced a clone of its own consisting of thousands of individuals. The striking fact is that the average size of individuals in the two clones is the same. In each there are large individuals and small individuals and all grades of intermediates. An attempt was made to produce a large race by selecting only the largest individuals as the starting point of new clones and repeating this for a long time, but the attempt was a failure. No better success was had in attempting to produce a small race. The reason for these failures is that no change had occurred in the hereditary materials of the stock and that the observed differences in individuals were all merely environmental modifications, which are not hereditary. A series of generations resulting from repeated fissions is an example of a PURE LINE, one in which all individuals are genetically identical. They are said to belong to the same GENOTYPE, or to be genotypically identical. On the other hand, it was found that when different clones were produced, each from a single individual isolated from a wild stock, that some individuals in one clone were visibly identical with some individuals in another clone. That is, they were phenotypically alike, but they will produce clones that are genotypically different, having a different average size of individuals. Several individuals that look alike are said to belong to the same PHENOTYPE, or to be phenotypically identical, even if they do not breed alike. This distinction between phenotypes and genotypes is one of great importance in understanding the complex situations soon to be described in connection with sexual reproduction.

What has been said about pure-line heredity in animals that reproduce by fission holds equally well for those animals, such as Hydra, that reproduce by budding, for a bud is no more than a branch given off from a parent body. A family of hydras derived from a single individual by budding constitutes a typical clone. When Hydra reproduces sexually, however, quite a different situation presents itself.

3. *Parthenogenesis*

Many species of animals reproduce from eggs without the latter being fertilized. Thus in aphids (plant lice) the first female of the parthenogenetic series produces a generation of females, and these produce nothing but females. For many generations there is a succession of females and no males. After a time a change takes

place in the hereditary material (chromosomes) and some males are produced, and then sexual reproduction intervenes for one generation.

As long as there is no fertilization of eggs, however, all the individuals in such a pure line are genetically the same and the individuals, because they have the same hereditary constitution, are all females and alike in most other respects. They may differ in size or in other ways, but these differences are not hereditary. In these types of parthenogenetic forms no reduction division takes place and offspring receive the same chromosome complex as that present in the parent. They, therefore, constitute a true clone. There are, however, other types of parthogenetic animals (e.g., bees and wasps) in which the reduction division does occur and therefore pure heredity is interfered with. Such types need not be considered in this connection.

4. *Twinning*

In the discussion of Reproductive Mechanisms (Chapter XLIII) twinning was described as a somatogenic method of reproduction under the subhead of longitudinal fission. As a special example of one-egg twinning the peculiar case of the nine-banded armadillo (Fig. 252) was presented. The essence of this situation is that from a single zygote an embryo is produced which is at first like any normal mammalian embryo, but this embryo at a rather early stage multiplies itself by somatic division into four embryos. Such a group of offspring constitutes a clone and is a short pure line, for all individuals in a given set of quadruplets are genetically identical. All in a given set are of the same sex and are extremely similar, differing from one another only in such minutiæ as the number of scales in the armor or slight differences in size.

A similar situation is present in man. We are all familiar with the fact that identical twins are not infrequently born and that even identical triplets and quadruplets are occasionally produced. Much evidence supports the view that identical twins, etc., are derived from a single zygote and are therefore genetically identical. A great deal of attention has been paid to the degrees of resemblance and difference present in these genetically identical individuals. They show us what may be expected in the way of variability when heredity is undisturbed by the sexual mode of reproduction.

Identical twins are startlingly similar, so much so that they are difficult to distinguish apart, but accurate measurements and detailed comparisons have shown that they differ slightly in many finer points. They differ, in fact, to just the same extent as do the right and left sides of a single individual. Thus their finger prints are at least as similar as are those of the right and left hands of a single individual. Their teeth are equally similar, as are their ears, their eyes, and many other features. But the most striking fact is that they are essentially duplicate individuals. Identical twins give us a true picture of what the world of life would be like without sexual reproduction. If human beings reproduced asexually we might expect whole family connections to be composed of individuals as nearly uniform as are identical twins. Contrast this hypothetical situation with that which actually exists, namely, that even brothers are often very different, and one will realize that most of the diversity within a family, a race, or a species is due to the diversity mechanism and not to heredity proper. Heredity is a powerful force in evolution, a force that tends to bring about persistence of type and uniformity of progeny. It accounts for the fact that general body plans and many homologous structures persist over long periods of time. Heredity is the conservative factor in evolution, tending to inhibit change or progress, but fortunately there are equally powerful forces working in the opposite direction, tending to introduce new characters and to bring about an infinitude of varied combinations of characters already present. We shall now deal with these mechanisms of diversity and change.

B. Heredity with Genetic Variability

Unit Characters and Genes

In striking contrast with the type of heredity found in connection with asexual modes of reproduction is the prevailing and more familiar type of heredity that obtains in all forms of animals and plants that employ the sexual mode of reproduction. In these forms a pair of parents, instead of producing offspring all as similar as identical twins, produce such a variety of offspring that heredity seems at first sight quite a haphazard phenomenon, without rhyme or reason. It had long been realized that a son does not inherit all his traits from father alone or mother alone, but inherits

certain unit traits from one parent and some from the other. It was commonly said of a person that "he has his father's eyes, and his mother's nose, but his chin is more like his grandfather's." Thus it was vaguely felt that characters are inherited as though each is a separate item that could be passed on independently of others. ***Gregor Mendel*** was the first to put this general impression into the form of a definite law, the LAW OF UNIT CHARACTERS. He stated that there are large numbers of separate hereditary characters that are inherited independently of each other so that the offspring can inherit any combination of the various character differences of the two parents. Mendel decided to find out whether there were any rules or regularities as to the numerous combinations of parental characters that could appear in offspring. His genius lay in reducing the situation to its simplest terms, refusing to be confused by trying to untangle the complex intermixtures of large numbers of characters and confining his attention at the moment to one pair or a few pairs of contrasting characters. We shall soon see how he succeeded in reducing the chaos of our knowledge of biparental heredity to definite order.

Mendel happened to work with a material in which there were but few complications—the common varieties of garden peas—and he satisfied himself with the simpler aspects of the analysis of biparental heredity. To Mendel each unit character had a unit determiner in the germ plasm and the mechanism was simply one that sorted out these unit determiners according to certain fixed rules.

Subsequent workers, however, studied more complex cases and were forced to abandon the idea that any single determiner was solely responsible for a character. It soon came to be recognized that several or many determiners were responsible for the expression of a character. So any single hereditary unit was called a FACTOR instead of a determiner. More recently the term GENE has been substituted for the term factor.

Among the large number of geneticists who adopted Mendel's general methods one of them, ***T. H. Morgan,*** stands foremost. This indefatigable investigator, by specializing on one kind of animal (the fruit fly, Drosophila) for over a quarter of a century has thrown a flood of light on the whole mode of biparental heredity and the intimate cellular mechanisms responsible for the observed results. Out of Morgan's work has emerged a new theory,

not only a theory of heredity and diversity, but a more or less comprehensive theory of evolution in general, THE GENE THEORY, which we shall deal with in its proper place. But first we shall present an example of a relatively simple case of Mendelian heredity as seen in a common animal and shall interpret the results in the light of modern knowledge. Mendel lived and died before a knowledge of cellular mechanisms had been born. He had some hypotheses as to the mechanisms involved that were in a sense prophetic of the mechanisms discovered long after his death.

C. MENDEL'S LAWS AS SHOWN IN THE INHERITANCE OF COAT CHARACTERS IN GUINEA PIGS

Guinea pigs have long been among the favorite animals for experimental work in various branches of biology; hence it was but natural that they should be chosen for experimental breeding. Many fancy breeds have been produced and these possess many differentiating characters suitable for Mendelian analysis. Some of the varieties have been long bred from pedigreed stock, so that their genetic composition is known. Thus to start with we have certain homozygous races that breed true to certain characters. For example, there are pure breeding black races and pure breeding white, or albino, races; there are pure long-haired, or angora, races and pure short-haired races; there are pure smooth-haired races and pure rough-coated, or rosetted, races.

1. *Monohybrid Crosses*

If we wish to see the workings of the biparental heredity machine at its simplest, we should breed together two of these pure races differing in only one respect, say hair color. A pure black guinea pig—it makes no difference whether the black parent is the male or the female—is mated with a pure white individual. Somewhat to our surprise, if we were to perform this experiment for the first time, we would find invariably that all of the offspring would be black and none white. When these crossbred black individuals are interbred, brother to sister as is commonly done in animal breeding, we may be surprised to find that in addition to blacks there will be a definite proportion of pure whites. If large numbers of such experiments as the above are carried out, it will be found that there are three blacks to one white in the third generation.

The results of this experiment may be stated in tabular form as follows:—

P	(parents)	Black	$\times$	White
F_1	(first offspring generation)		All Black	
F_2	(second offspring generation)	3 Blacks		1 White.

In this diagram we have used the conventional terms most commonly used in describing Mendelian experiments. P stands for the parent generation; F_1 stands for the first hybrid generation or first filial generation; and F_2 stands for the offspring generation derived by interbreeding individuals of F_1.

In our experiment the white character disappears in the F_1 generation and only the black appears. We speak of the black character as DOMINANT and the white as RECESSIVE. The dominant character does not in any way destroy or affect the gene for white, but merely excludes it more or less completely from expressing itself in the body cells when both black and white genes are present in the same zygote. This is clearly brought out when, in the F_2 generation, the white character reappears pure in one fourth of the offspring. A recessive character is therefore one that can express itself fully only in the absence of the alternative or homologous dominant character. Recessives are therefore HOMOZYGOUS or pure breeding.

Before we can proceed very far with our analysis of Mendelian heredity we must, for the sake of clearness and brevity, adopt some of the stock conventions that are now recognized as standard. In attempting to formulate the representatives of character differences in the germ cells it is customary to represent the dominant character gene by a capital letter, usually the initial letter of the name of the character of which the gene is the differential, while the recessive is represented by the corresponding small letter. We may then restate the above experiment in terms of the genes involved:—

P (zygotes)	BB	$\times$	bb
P (gametes)	B		b
F_1 (zygotes)		Bb	
F_1 (gametes)	B	and	b (for both eggs and sperms)
F_2 (zygotes)	1 BB;	2 Bb;	1 bb (the F_2 genotypic ratio).

Several important principles are illustrated by this formulation: *a*, both of the parents are shown to contain two coat-color genes of the same kind and are therefore homozygous for that character; *b*, the reduction division results in gametes with only one gene of the kind possessed by the parent; *c*, the F_1 zygotes are all HETEROZYGOUS, containing both B and b; *d*, the gametes of F_1 are pure with respect to either B or b, never having both in any one gamete; *e*, just half of the gametes of F_1 possess B and half possess b; *f*, if the male and female gametes unite by chance, the following combinations will occur with equal frequency—BB, Bb, bB, bb; *g*, but Bb and bB are the same, and therefore this combination occurs twice as frequently as either of the other two, BB or bb; *h*, there is little if any difference in appearance between the individuals having the zygotic combinations BB and Bb, and we have to lump together all individuals of both kinds as blacks, thus accounting for the PHENOTYPIC RATIO of 3 blacks to 1 white.

The only sure way of assorting the blacks of the F_2 generation into the two groups, homozygous and heterozygous, is to breed each of them with a white. If the black individuals are homozygous, all offspring will be black; but if the black individual is heterozygous, half of the offspring will be heterozygous black and half white, for the chances of a white gamete meeting with a black or with a white gamete are equal.

It is easy to carry out Mendelian experiments to the F_3 and the F_4 generations, but nothing new in principle is revealed; for the homozygous individuals, BB and bb, always breed true, while the heterozygous individuals, Bb, always split up into the three groups —1 BB, 2 Bb, 1 bb.

The same analysis as the above can readily be made for all other pairs of homologous hereditary units. Thus, in the case of the character HAIR LENGTH, where short hair is found to be dominant over long hair, we would arrive at the following formula:—

P (zygotes)	SS	×	ss
P (gametes)	S		s
F_1 (zygotes)		Ss	
F_1 (gametes)	S	and	s (in both eggs and sperms)
F_2 (zygotes)	1 SS;	2 Ss;	1 ss (the F_2 genotypic ratio).

It is also found by experiment that rough, or rosetted, hair (R) is dominant over smooth hair (r). A formula for this cross would

be essentially the same as those given above for hair color and hair length.

MONOHYBRID CROSSES are those like the three just described, where only one pair of differentiating characters exists (or is to be

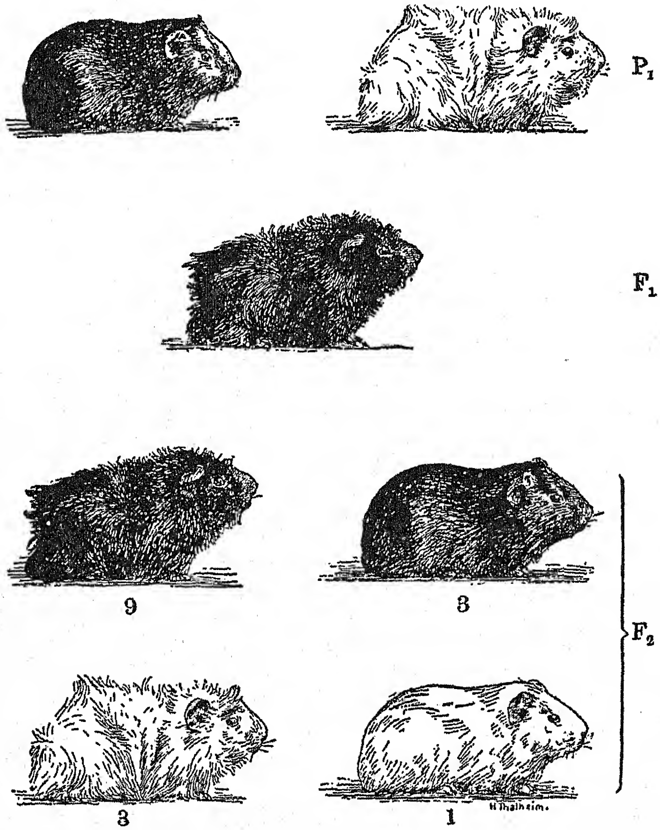


FIG. 274. Pictorial diagram of a dihybrid cross, showing the results of crossing black smooth and white rough guinea-pigs. F_1 is black rough. F_2 is in the ratio 9 black rough: 3 white rough: 3 black smooth: 1 white smooth. (From Babcock and Clausen, after Baur.)

considered) in the analysis. While each pair of characters, when considered by itself, behaves just like those already considered, much new light has been thrown upon the nature of the heredity machine by following the simultaneous inheritance of two or more pairs of characters. We speak of a cross involving two pairs of

differentiating characters as a DIHYBRID CROSS and of one involving three pairs of different genes as a TRIHYBRID CROSS.

2. *Dihybrid Crosses*

Let us consider the simultaneous inheritance of two of the pairs of different characters that have been dealt with separately; namely, those of hair color and hair form. For the parents we might select one (either male or female) guinea pig with, say, white rough hair, and another guinea pig with black smooth hair (Fig. 274). Since black is dominant over white and rough dominant over smooth, we would have the following formulation:—

P (zygotes)	BBrr	×	bbRR		
P (gametes)	Br		bR		
F_1 (zygotes)		BbRr			
F_1 (gametes)	BR,	Br,	bR,	br	(in equal numbers in both eggs and sperms)
F_2 (zygotes)	9 black roughs; 3 black smooths; 3 white roughs; 1 white smooth (the dihybrid phenotypic ratio for F_2 generation).				

The genotypic ratio for the F_2 zygotes is best represented by the so-called PUNNETT SQUARE, as follows:—

	SPERMS OF F_1 BR	Br	bR	br
BR	BR BR	BR Br	BR bR	BR br
EGGS OF F_1 Br	BR Br	Br Br	Br bR	Br br
bR	BR bR	Br bR	bR bR	bR br
br	BR br	Br br	bR br	br br

There are two ways of interpreting this formulation: phenotypically and genotypically. If we are concerned merely with appearances or with the characters of the single generation, we can obtain the phenotypic dihybrid ratio rather easily as follows: All of the zygotes, represented one to a square, that contain both

dominant characters, B and R, irrespective of the presence of the recessive characters, will appear to be black and rough. Of the sixteen squares—each of these constitutes one out of every sixteen possibilities of the union of the four kinds of gametes concerned—nine will be found to contain both B and R; three contain B but no R; three contain R but no B; and one contains neither R nor B. This would account for the phenotypic ratio of: 9 black roughs; 3 black smooths; 3 white roughs; and 1 white smooth, which is a typical example of an F_2 dihybrid, phenotypic ratio and is illustrated graphically in Figure 274.

Now it is clear that, on the basis of the genes present, there are four kinds of black roughs: those homozygous for both B and R, those homozygous for B but heterozygous for R, and those homozygous for R but heterozygous for B and those heterozygous for both B and R. Similarly, there are two genotypes for the phenotype black smooth: those in which B is homozygous and those in which B is heterozygous. Again, there are two genotypes of the phenotype white rough: one in which R is homozygous and one in which R is heterozygous. Finally, there is but one genotype of the phenotype white smooth, for both white and smooth are homozygous, else they would not be able to appear.

3. *Trihybrid Crosses*

It is not difficult to go one step further in the process of following paired characters simultaneously and to work out the ratios for the inheritance of three pair of independently segregating characters. We can most readily do this by simply adding one more pair of contrasting characters to the two pairs already dealt with, using as the additional character that of hair length, involving the dominant gene for short fur (S) and the recessive gene for long fur, designated s. In this case we shall have to be satisfied to go no further than a phenotypic analysis, for though the genotypic analysis as based on a Punnett square is not difficult, it is rather cumbersome for present purposes. Diagramming the experiment, we obtain the following formula:—

P (zygotes)	BBSSrr	+	bbssRR
P (gametes)	BSr		bsR
F_1 (zygotes)		BbSsRr	
F_1 (gametes)	BSR, BSr, BsR, bSR, Bsr, bSr, bsR, bsr (equal numbers of each kind in both eggs and sperms)		

F_2 (zygotes) 27 black short rough; 9 black short smooth; 9 black long rough; 9 white short rough; 3 black long smooth; 3 white short smooth; 3 white long rough; and 1 white long smooth. This is the typical F_2 trihybrid phenotypic ratio.

By the use of the Punnett square the student can readily work out the genotypes concerned in each of the phenotypes.

D. The Mechanism of Simple Mendelian Heredity (The Gene Theory)

From the formulations showing the various gene combinations in the several types of crosses just described one could work out a hypothetical mechanism for the germ cells that would be necessary in order to explain the results. For a long time the actual mechanism was unknown, but soon after the rediscovery of Mendel's work in 1900, it was discovered that the key to the problem lay in the chromosomes of the germ cells and in the events involved in those parts of the germ-cell cycle which we have spoken of as synapsis of homologous chromosomes and their segregation in such a way that only one of each pair goes to each gamete, involving a reduction of the number of chromosomes to half that characteristic of body cells. In a monohybrid case such as that described for black versus white coat color we must assume that in individuals of the F_1 generation each unreduced germ cell has two chromosomes carrying genes for coat color. One of these has only the gene for black (B) and the other only the gene for white (b). When the gametes are formed half of them get the B-bearing chromosomes and half get the b-bearing chromosomes. Each parent, then, has equal numbers of B-bearing and b-bearing gametes, which tend to unite at fertilization in random fashion, each kind of sperm having equal chances to fertilize each kind of egg. One can readily see that once out of four times a B-bearing egg and a B-bearing sperm will unite, once out of four times a b-bearing egg and a b-bearing sperm will unite, and twice out of four times B-bearing gametes will unite with b-bearing gametes. This will give the ratio of 1 BB zygote: 2 Bb zygotes: 1 bb zygote, which is nothing else than the genotypic ratio that actually occurs and had already been formulated on the basis of breeding results. Since the observed breeding results accord so perfectly with the known facts as to the chromosomal mechanism it seems reasonable to attribute the former to the latter and to state that the chromo-

somal mechanism is the cause of the regularities found in breeding.

In order to account for the dihybrid and trihybrid ratios it is necessary to assume that the two or three pairs of alternative characters involved (such as the different coat colors, the different arrangements of hair, and the different hair lengths) are determined by genes that lie in as many different pairs of chromosomes. Moreover, it is necessary to assume that at the time of the reduction division the two or three pairs of homologous chromosomes involved place themselves in the division spindle quite independently of each other and that the arrangement taken at any time is a matter of chance. In other words, if two pairs of chromosomes in a dihybrid F_1 generation are involved in the reduction division (the B-bearing and the b-bearing chromosomes being one pair and the R-bearing and r-bearing chromosomes being the other pair) there are equal chances of both dominant genes going to the same gamete and of the two different dominants going to different gametes. So there will be four different gametes in equal numbers, two from the first possible arrangement (BR and br) and two from the second (Br and bR). This will result in the next generation in the various kinds of zygotes shown in the Punnett square on p. 585.

By simply including a third pair of genes in a third pair of chromosomes, say S for short hair and s for long hair, we get an F_1 hybrid type with the following formula in its body cells and unreduced germ cells (Bb, Rr, Ss). Since the homologous genes segregate into gametes independently, the following eight kinds of gametes will be produced in equal numbers (BRS, BRs, BrS, bRS, Brs, bRs, brS, and brs). Both males and females of the F_1 generation having equal numbers of each kind of gamete there will be 8×8 zygote combinations in equal numbers, some of which will be duplicates.

Each additional pair of genes in an additional pair of chromosomes will double the number of kinds of gametes. For example, when the original parents differ from each other with regard to four genes, one parent being pure for dominant genes A, B, C, D, and the other pure for the recessives, a, b, c, and d, the segregation of these four kinds of genes into gametes will occur as in Figure 275. It will be seen that there are sixteen possible gene combinations in the gametes of the F_1 generation, double the number found in the trihybrid experiment.

With additional pairs of gene differences, each in another pair of chromosomes, doubling of the number of different kinds of gametes occurs. Thus if only ten different pairs of chromosomes carrying gene differences are involved there are produced 1024 different kinds of gamete combinations and a huge number of different possible zygotes. Imagine the tremendous possibility of diversity in

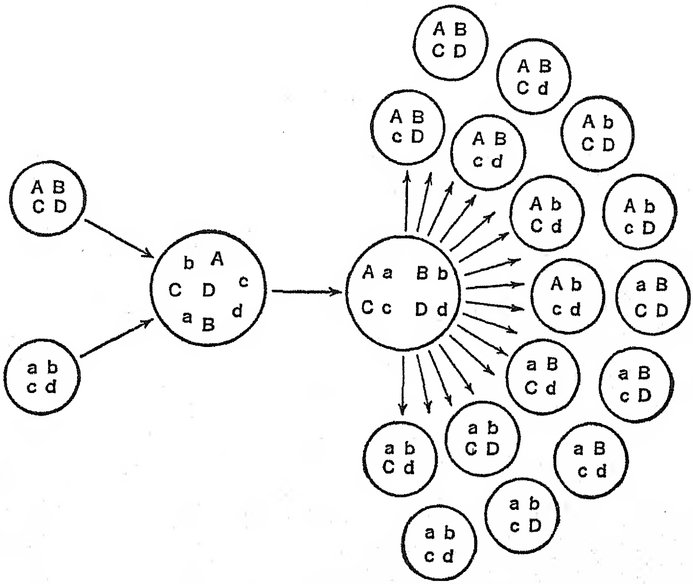


FIG. 275. Diagram to show the union of simplex groups of either the chromosomes or of the genes of the gametes to form the duplex condition of the zygote and animal body; and then their pairing at synapsis, and segregation in the gametes. With four pairs of chromosomes or of genes (Aa, Bb, Cc, Dd) there are sixteen possible types of gametes. (From Woodruff, after Wilson.)

a species such as man, who possesses 24 pairs of chromosomes. The number of different gene combinations in the gametes runs up into the millions and the number of possible combinations of gametes to form new individuals runs up into almost astronomical figures. No wonder then that duplicate human beings never occur unless a single zygote divides to produce two individuals, as is the case in identical twins.

We have just described the diversity machine at work. Such diversity combined with pure heredity of individual genes is the

product of the mechanisms of sexual reproduction. All this mechanism does is to shuffle and deal out all possible combinations of independently inherited genes. Nothing new is added to the sum of hereditary units, but all sorts of combinations of those present can readily be produced.

It is possible to get all the best genes of the father and mother stocks combined in one child, or all the worst. But the usual outcome is that the child gets a combination of the good, the bad, and the indifferent genes. If a bad character has as its basis a recessive gene and the individual has also the dominant of the same gene pair, the poor character may not express itself, but if two persons heterozygous for a poor trait were to mate, the chances are one out of four that an offspring will receive the recessive gene from both parents and will express the bad character. This is one reason why sometimes two phenotypically normal parents, especially if they are cousins, may have one or more defective offspring.

This would be a fascinating subject to pursue further but it has been found advisable in a general course to go no further into the subject of Mendelian heredity than we have gone. Students interested in going on in Genetics will usually find courses in this subject offered in departments of Zoölogy or Botany.

Before leaving the subject of Mendelian heredity, however, just a glimpse of the vistas looking toward advanced genetics might be given. It has been found, for example, that no unit character is determined by a single gene, but that several or perhaps all the genes are involved more or less. Further, it has been found that there are many genes in each chromosome, that they are arranged like a chain of beads placed lengthwise in a chromosome and that homologous genes frequently cross over from one chromosome to its partner when they are paired in synapsis. This crossing over greatly increases the possibility of different gene combinations and therefore constitutes an additional mechanism for increasing diversity. The foregoing statements are made possible chiefly through the long-continued and epoch-making experiments with the fruit fly, Drosophila, conducted by T. H. Morgan and his associates. It is also chiefly through their work that we have attained much of our present knowledge of the Change Factor (Mutation) which will next be discussed.

E. Mutation

We have seen that the sex mechanism is capable of grinding out an almost limitless number of combinations of characters already present in the species, but that the unit characters (or more properly, the genes) remain constant except for occasional disturbances either of individual genes or of whole chromosomes or parts of the latter. While genes may be regarded as extraordinarily stable and chromosome numbers in a species are rarely changed, it has been found that most genes do change sooner or later and that changes in whole chromosomes or parts of the latter occasionally do occur in a few individuals. We recognize two kinds of genetic changes, that are sometimes spoken of as Gene Mutations and Chromosomal Mutations.

1. *Gene Mutations*

More than a quarter of a century ago, Morgan began his study of evolution of the fruit fly with the main motive of finding out whether he could observe the first appearance of new characters in a rapidly breeding species in which one could get a new generation every two weeks. After breeding from one pair of flies a number of generations involving many thousands of individuals, one day he discovered a fly with white eyes (the typical eye color is red). This fly, a male, was mated with a red-eyed female and the individuals of the F_1 generation were all red-eyed, but when F_1 males and females were interbred, they produced offspring three fourths of which were red-eyed and one fourth white-eyed. (The fact that all the white-eyed individuals were males need not concern us here.) The three red to one white ratio is the familiar F_2 phenotypic ratio characteristic of a monohybrid cross. Hence it was obvious that what had happened was a change in one gene for eye color from the dominant to the recessive state. The white-eye condition behaves as a recessive unit character. Not long afterwards another fly was observed that had yellow body color instead of the gray color typical for the species. This proved to be inherited in the same fashion as the white-eye character, and the effect was attributed to a recessive mutation of another gene. As the months and years went by various other mutant flies occurred one at a time, until now over three hundred different MUTANTS have occurred in this one species.

The changes involved in the various mutants were all shown to be due to changes in single genes. They affected all sorts of bodily characters: eye color, body color, wing shape, body bristles, the legs, the presence or absence of eyes or wings, and numerous other characters. The appearance of a few of the best known mutants of Drosophila are shown in Figures 276 and 277. Other mutations

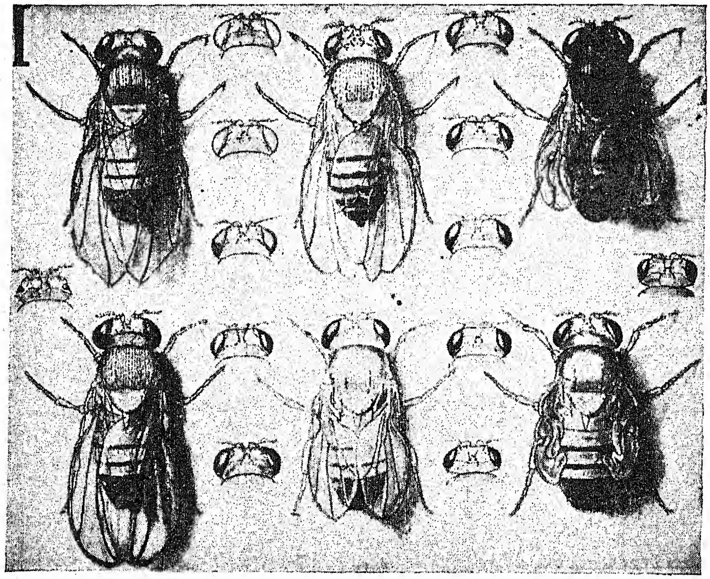


FIG. 276. Mutants of *Drosophila melanogaster*, showing changes in wings, body, eyes, legs. (From Morgan.)

involved changes in the physiology of the individual, some of them producing death in individuals homozygous for the mutant gene.

On the whole it must be said that most of the gene changes were harmful in their effects, a considerable number were indifferent, while a very few might be regarded as beneficial—at least if presented with a somewhat different environment. Thus the mutant known as "ebony," involving a black body, might be beneficial if the animals lived in such regions that they would be better protected from enemies because of resembling a dark background. One must admit, however, that it is difficult to see how any of the mutants observed in Drosophila are better adapted to present conditions than are the normal flies. Perhaps, however, this is just what we should expect in view of the fact that the genus

Drosophila has been going on possibly for millions of years and has been mutating all this time. Hence it seems probable that all the unit characters it now possesses represent the best mutations that have appeared during its evolutionary history. With more or less random mutation occurring as it does, one would hardly expect a new character to occur in twenty-five years of breeding that is

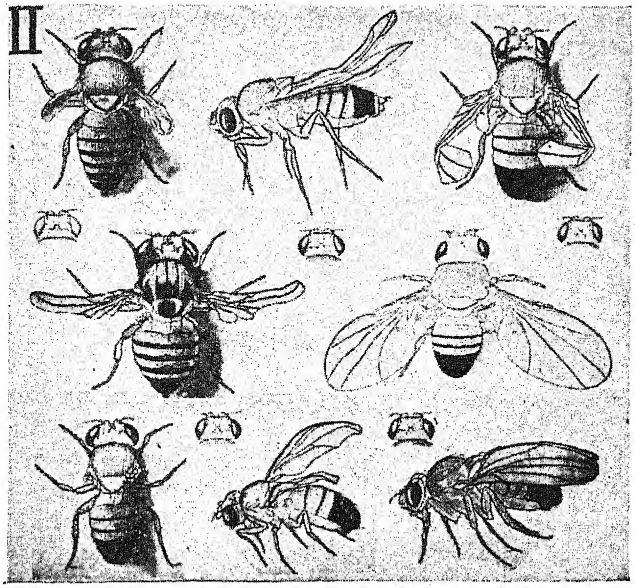


Fig. 277. Further mutants of *Drosophila melanogaster,* showing chiefly wing mutations. (From Morgan.)

superior to any of those that have been acquired through the ages and have run the gauntlet of competition so successfully. If too many improvements had been found in the experimental stocks, this would have spoiled the gene mutation theory, for, obviously, a true evolutionary mechanism should not work so rapidly.

Gene mutations have now been found in a large number of animals and plants, and their hereditary behavior has turned out to be like that described for Drosophila. Some mutations are dominant, some recessive and some intermediate (a condition in which neither the old nor the new character tends to suppress the other in the F_1 generation, but an intermediate condition is expressed).

All gene mutations are inherited according to Mendel's Laws. From this we may conclude that whenever we find differences that

follow the Mendelian plan of inheritance, such differences are due to differences in genes. In man, for example, it is frequently found that a bodily peculiarity, such as an extra finger on the hands, is inherited as a simple dominant unit character. The inference that seems legitimate is that the extra-finger character (polydactylism) has arisen as the result of a mutation of a single gene in some ancestor. Numerous other human peculiarities belong to the same category as polydactylism.

2. *Chromosomal Mutations*

Various kinds of gross or slight changes, involving not single genes but whole sets of chromosomes, single chromosomes, and parts of a chromosome, have been found to occur and to carry with them important changes in bodily characters. Such genetic changes are called by some geneticists chromosomal mutations. This type of mutation is especially common in plants and is the type emphasized by ***Hugo de Vries,*** the original discoverer of mutations. Although chromosomal mutations appear to be a cause of new species in many plants and some animals, geneticists in general regard this type of mutation as secondary in importance to gene mutations as an evolutionary mechanism. For that reason we shall pass over this subject rather lightly. It should be said, however, that at least one type of chromosomal mutation deserves to rank relatively high as a true factor in evolution, namely, that type known as POLYPLOIDY. This type of mutation involves an abrupt doubling of the total number of chromosomes. Many species of the same genus have chromosome numbers that are multiples of some simpler number and it is assumed that these species have arisen through repeated doubling of the chromosome number of the ancestral species from which they are believed to have been derived. So we may conclude that polyploidy has been responsible for a good deal of SPECIATION, or the production of new species. How important this mechanism is as compared with that of gene mutations, it is at present impossible to decide.

3. *The Causes of Mutations*

Quite naturally one asks himself what makes the genes change in order to give rise to mutations, and what causes germ cells to change their chromosome numbers?

As a matter of fact, the genes are very resistant to the effects of environmental changes. Were they easily changed, species would be extremely unstable, changing rapidly before our eyes. It has been calculated that in Drosophila only about one gene mutation occurs to three hundred gametes, so that a particular gene would change in only one out of about a million gametes. If one has first taken the trouble to discover the normal rate of gene mutations he is then in a position to attempt to change this known rate by experimental means. In 1926 *H. J. Muller,* after trying various means of getting at the genes, finally succeeded, by exposing flies to X-rays, in increasing the normal rate of mutation in Drosophila one hundred and fifty fold. But all he seems to have been able to do was to change the *rate* of appearance, not the *kinds* of mutations. Nevertheless this great increase in the number of mutations per generation vastly increased the amount of material for study and has accelerated the progress of genetic research very greatly. Were X-rays a normal feature of environment it might be concluded that mutations in nature are caused by these rays, but unfortunately there are no X-rays in nature. It was, however, also possible greatly to increase the rate of mutations with radium emanations, but again, it seems that there is little chance of organisms being materially affected by the rather poor supply of radio-active substances in nature. As soon as the now famous Cosmic Rays were discovered, geneticists began to wonder whether these ever-present rays might not be responsible for mutations. It was proposed to take up a stock of pedigreed Drosophilas in the stratosphere balloon to see whether the more abundant cosmic rays of the upper atmosphere would increase the rate of mutation. So far as we know, this promising experiment has not been tried.

Muller and other workers have claimed that a very slight increase in mutation rate in Drosophila has been induced by subjecting animals to rather high temperatures. It would be premature to discuss these results until they have been confirmed in an adequate way. It has also been claimed that the appearance of polyploidy is traceable to sudden changes in temperature, but these claims have as yet not been satisfactorily proved.

On the whole then, it may be said that, at present, we are very much in the dark as to the causes of mutations in nature. This is now one of the most important of the unsolved problems of biology.

SUMMARY

1. Pure heredity, uninfluenced by the diversity-increasing mechanism of sexual reproduction, may be studied in many forms that exhibit certain modes of asexual or somatogenic reproduction.

2. Examples of vegetative propagation (fission, budding, parthenogenesis, and twinning) are described. The feature common to all of these is that all offspring of a given parent are genetically identical, both with their parent and among themselves.

3. When offspring are all alike genetically they constitute what is known as a pure line or a clone.

4. An examination of the nearly complete identity of members of a pure line, such as a pair of identical twins, shows how little evolutionary change could be expected in a species that reproduces without employing the methods of sexual reproduction.

5. The mechanisms of sexual reproduction are specifically: *a*, the pairing of homologous chromosomes (synapsis) and the segregation into individual gametes of only one of each kind of chromosome and their contained genes, and *b*, the random union of male and female gametes.

6. These mechanisms are responsible for what is known as SEGREGATION and the PURITY OF GAMETES, which means that the gametes derived from a parent heterozygous for any pair of contrasting genes can receive only one of the two kinds of genes of any given pair. That is, the gametes cannot be hybrid, but must be pure for one or the other of two alternative genes.

7. The way in which one pair of contrasting genes is distributed to gametes is entirely independent of that of other contrasting genes. This gives rise to the LAW OF RANDOM ASSORTMENT of genes into gametes and accounts to a large extent for the great variety of combinations of characters found in the progeny of hybrids (or individuals differing genetically in a number of unit characters).

8. The RANDOM RECOMBINATION of the various assortments of genes from two parents still further increases the diversity of offspring.

9. The monohybrid, dihybrid, and trihybrid ratios found in the F_2 generation of Mendelian breeding experiments are readily accounted for by the known behavior of chromosomes in the reduction division and in fertilization.

10. The tremendous diversity of human beings, for example, is believed to be due largely to the mechanisms of sexual reproduction outlined above.

11. The sexual method of producing diversity does no more than combine genetic units in a great variety of ways. It does not produce changes in the units of heredity (genes) themselves.

12. Genes do, however, change occasionally, and whenever they do change they produce mutants, or individuals with some characters different from those of the parent stock. A gene mutation is either a dominant or a recessive change and is inherited according to Mendel's Laws just as are the typical characters of the species.

13. Character differences that are inherited according to Mendel's Laws are regarded as having arisen by gene mutations.

14. Chromosomal mutations, especially those involving polyploidy (a doubling of the whole chromosomal number), are not uncommon and are regarded by some as responsible for the origin of some new species, especially of plants.

15. We do not know as yet what causes mutations, but experimenters have succeeded in greatly increasing the rate of mutation by X-rays and radium emanations. It has been suggested, but never proven, that cosmic rays might be the natural cause of gene mutations. The problem of the real cause of mutations is unsolved.

CHAPTER L

OTHER CAUSAL FACTORS OF EVOLUTION

A. Guiding Factors

As we have already seen, the heredity factor, working alone, tends to prevent evolution altogether. The diversity factor produces a perfectly random array of combinations of hereditary units, good, bad, and indifferent combinations being equally likely to be produced. The mutation factor introduces a vast number of genetic changes, most of which are bad, some indifferent, and a few conceivably good. There is nothing inherent in these mechanisms to favor progressive or orderly change and nothing to account for the fact that, on the whole, organisms are well adapted to their environment and that there exist many adaptive mechanisms in animals and plants that are very specially adjusted to certain features of the environment. Obviously then, guiding factors of some sort must have been at work in order to have brought about whatever of orderly change and of adaptiveness has resulted from the evolutionary process. Three main theories have been advanced to explain the orderliness and adaptiveness of evolution: 1, Natural Selection (a theory of ***Charles Darwin***), 2, The Inheritance of Acquired Characters (a theory of ***Jean-Baptiste Lamarck***), and 3, various Orthogenesis Theories. These we shall briefly consider in the light of modern knowledge, and especially as they may be regarded as operating in connection with the factors already discussed.

1. *Natural Selection*

Darwin proposed his theory long before the science of Genetics had developed. He assumed that, because all species tend to overproduce, many individuals must perish; that all individuals vary with regard to all their characters; that all character differences (even somatic modifications) are hereditary. On the basis of these assumptions he concluded that the best adapted individuals in each generation tend to survive and to be the parents of the next gen-

eration; that the characters which had aided the survival of the parents would all be passed on to offspring; and that there would be a steady increase of the sum total of adaptive characters from generation to generation.

Thus Natural Selection would act as an arbiter over the fate of all individuals, tending to preserve those with the most highly adaptive complexes of characters and eliminating those with the least adaptive complexes. If such a factor were to operate in this way one could understand very easily not only why evolution must give rise to better and better adaptive types, but also how progress would be orderly and go steadily in certain definite directions. The usual picture aroused in the mind of the reader when confronted with the Natural Selection concept is that of a violent struggle for existence among individuals of a species, and a survival of the victors in this struggle. Modern geneticists, however, on the basis of the Gene Theory, paint for us a more peaceful scene. ***T. H. Morgan,*** commenting on these two contrasting pictures of evolution, remarks that: "Such a view (meaning that involved in the Gene Theory) gives us a somewhat different picture of the process of evolution from the old idea of a ferocious struggle between individuals of a species with survival of the fittest and annihilation of the less fit. Evolution assumes a more peaceful aspect. New and advantageous characters survive by incorporating themselves into the race, improving it, and opening up to it new opportunities. In other words, the emphasis may be placed less on the competition of individuals of a species (because the destruction of the less fit does not in itself lead to anything new) than to the appearance of new characters and modifications of old characters, that become incorporated in the species, for on these depends the evolution of the race."

Since mutations are at present the only certainly known types of hereditary change, the introduction of new characters must depend on them. Now it is well known that species, when they change into new species, change as a group. Evolution is a matter of changing populations, not changing individuals. When a given gene changes in one individual in a population of a thousand there is no chance of that gene in future generations appearing in more than one in a thousand individuals unless the same mutation is repeated again and again. The fact that gene mutations do repeat themselves over and over again at a rather steady rate may ex-

plain how a new character may gain slowly in prevalence as compared with an old character. But reverse mutations of the mutant gene back to the old condition also occur, though at a slower rate than do original mutations. The result would be no more than an equilibrium in the prevalence of new and old genes and no further progress would be made by the new gene unless helped by another factor. It is here that Natural Selection would come into play. If a mutant character is adaptively at all superior to the nonmutant character it will gain in prevalence because individuals with the new gene will survive in somewhat larger numbers and will therefore produce more offspring. Natural Selection then will, in such a case, exert a steady pressure favoring an increase in the relative proportion of mutated as against nonmutated genes in the species. In the course of time the mutant genes might entirely crowd out the nonmutant ones and the whole species become homozygous for the once rare mutant character. Various other factors might influence the relative proportions of mutant as against nonmutant genes, but a consideration of them in this place would lead us too deeply into a technical field.

In conclusion, then, we may say that Natural Selection in its present aspect is regarded as a factor that merely affects the relative proportions of numerous pairs of rival genes in their slow but certain competition to be incorporated into the species germ plasm. The bodily differences produced by some gene mutations are so damaging that the individual cannot survive (we refer to lethal mutations), others involve serious debilities of one sort or another, still others seem to have no special adaptive significance. It is easy to see how the lethal mutant genes would be kept down to a safe minimum, and how those that are not fatal but merely debilitating would decrease in their relative frequency, and how the rare and occasional mutants that introduce improvements would come slowly but inevitably to crowd out their rival genes. Think of this kind of shifting in relative proportions of rival gene pairs as not involving one gene pair, but perhaps thousands of them at once, and our picture of Natural Selection becomes a very complicated one.

One may judge from the last few paragraphs that our real knowledge of this factor of evolution is slight as compared with that concerning the factors dealt with in the last chapter. Nevertheless this old theory of Darwin in its modern dress is the best

explanation of the orderly and adaptive trends of evolution that has yet been presented.

2. *The Inheritance of Acquired Characters*

Because of the fact that very few biologists today regard Lamarck's theory with favor, we shall give it only scant attention. The central idea of Lamarck's attempt to explain the adaptive character of evolution is that organisms respond to changes in the environment in ways that adjust them to such changes, and that organs function in such a way as to improve their performances by practice. Moreover, Lamarck thought that improvements made by individuals in the manner just stated are transmitted by heredity to offspring. The latter, starting where the parents left off, or at least with some of the parents' acquired improvements, would improve still further. Thus from generation to generation the adaptive characters would be more and more highly perfected through the accumulation of the gains made by each successive generation.

Now the kinds of improvements contemplated by Lamarck are what we have already called somatic modifications, and these we have already adjudged to be nonhereditary, since they are not changes in the germ plasm. Theoretically, then, they should not be passed on from parent to offspring. Scores of experiments have been performed that were designed to test whether or not somatic modifications can affect the germ plasm and thus be passed on. None of them so far have given results that are regarded as proof of the inheritance of acquired characters. At the present time then, although many biologists would be glad to accept Lamarck's theory, they are unable to do so because all of the experimental evidence is against it and none definitely for it.

3. *Orthogenesis Theories*

Even less need be said about orthogenesis theories than was said about Lamarck's theory. According to orthogenesis theories, the reason why evolution has followed some very definite trends, as for example those seen in the evolution of the horse tribe, is that the germ plasm has inherent in it a certain directive force that requires evolution to follow certain straight pathways of change. No one has the slightest idea as to the nature of the directive forces involved. Some biologists with vitalistic leanings have gone

so far as to assume that the germ plasm has a sort of organic purpose that enables it to plan its course, but such an idea is so foreign to science that we shall not entertain it even for a moment. We prefer to leave orthogenesis for the consideration of philosophers. The concept is of little use to us in our attempts to explain the mechanisms of evolution.

B. The Dividing Factor (Isolation)

If we imagine a species slowly changing its character through the action of the diversity-increasing factor, the mutation factor and Natural Selection, we would expect this species to advance as a whole and to change as a whole from one level to another. But the actual picture of evolution, as forced upon us by a consideration of the facts of taxonomy, is one that implies that species are continually splitting up first into varieties or races that ultimately grow up into new species. None of the preceding factors would, in themselves, have the power to split up species. Hence we need a dividing factor to account for SPECIATION, or the splitting up of old species into two or more new species. This is believed to be accomplished mainly by the factor of Isolation.

If all members of a species are free to interbreed without hindrance a species should evolve as a unit and should not split up, but if any sort of barrier is set up that tends to cut off a portion of a species from free interbreeding with the main population, the stage is set for a new species to arise.

A simple type of isolation is GEOGRAPHIC ISOLATION, according to which a few members of a species become shut off by a geographic barrier from the main population. Let us recall the account given in Chapter XLV of the numerous unique species on oceanic islands. The origin of such species is believed to have been about as follows:—A few insects (possibly only one fertilized female) were carried during a storm either in the air or in a floating log and were deposited on a small island far from the continent inhabited by the species in question. These then multiplied and produced a new population. Why should they be different from the members of parent species? In the first place, any small part of a population will differ from the whole in the proportion of its dominant and recessive genes. In the second place, the gene mutations occurring on the island may be different from those on the mainland. In the third place, the environment on the island

may favor the survival of certain mutants and thus cause them to increase their proportion in the population, whereas on the main land other mutants may be favored. The result would be that after a few centuries the two stocks would come to differ so much in their genetic content that they would be recognized by taxonomists as distinct species.

While geographic isolation is probably the most effective means of producing new species, there are many other kinds of isolation that may be nearly as effective. In this place we shall suggest only a few of these other means of isolation. If a species of plant, for example, differs among its individuals merely in the time of blooming, it is obvious that the early bloomers will be isolated from breeding with the late bloomers. This would tend to subdivide the species into two groups. Again, if one species of insect tends to exhibit two different kinds of food preference, those feeding on one species of plant would be more or less isolated, so far as breeding is concerned, from those feeding on another species of plant. And finally, if, as is often the case among higher animals, members of a single small community tend to confine their mating within their own circle, this would give the first opportunity for isolation to operate. After the small group had changed a bit, the tendency for restricted mating would be still stronger and splitting into two species would be well started. In conclusion, it may be said that most biologists consider isolation the chief factor in speciation, but that it is a relatively secondary evolutionary factor as compared with the other factors previously considered.

While we have discovered much about the mechanisms of evolution, there is still vastly more to learn. Who knows what future research may reveal?

SUMMARY

1. Among the various types of guiding factors proposed, Natural Selection is the only one that is regarded by biologists in general as satisfactory.

2. Natural Selection is now pictured not as a fierce struggle among individuals, but as a quiet pressure favoring the statistical proportions of various rival alternative genes in the germ plasm of whole populations.

3. There is at present a great deal of evidence against and practically no evidence in favor of Lamarck's theory of the Inheritance of Acquired Characters as a guiding factor in evolution.

4. Orthogenesis theories are at present little more than statements as to what seems to be a fact: that evolution has often followed rather definite

trends. The motive power, the character of which is utterly unexplained, is believed to be inherent in the germ plasm itself. Orthogenesis theories raise problems but do little to solve them.

5. Isolation is regarded as the most important factor in speciation (the origin of new species). Any factor that interferes with free interbreeding among all the members of a species would act as an isolation factor.

6. Geographic isolation, by cutting off one or a few individuals from the main stock, has apparently given rise to numerous peculiar species on oceanic islands.

7. Other less direct but none the less effective isolation factors are briefly discussed.

APPENDIX

BIBLIOGRAPHY

(The following list of books and monographs has been a constant source of reference for the author and would form a fairly comprehensive working library for a teacher of general Zoölogy.)

Babcock, E. B., and Clausen, R. E. *Genetics in Relation to Agriculture.* 2d edition. McGraw-Hill Book Co., 1927.

Bayliss, W. M. *Principles of General Physiology.* 3d edition. Longmans, Green & Co., 1921.

Calkins, G. N. *Biology.* Henry Holt & Co., 1917.

Calkins, G. N. *Protozoölogy.* Lea and Febiger, 1909.

Cambridge Natural History, The (a treatise in ten large volumes, covering the whole field of animals; valuable especially as a reference). The Macmillan Co.

Castle, W. E. *Genetics and Eugenics.* 3d edition. Harvard University Press, 1924.

Child, C. M. *Individuality in Organisms.* The University of Chicago Press, 1915.

Child, C. M. *Senescence and Rejuvenescence.* The University of Chicago Press, 1915.

Cockerell, T. D. A. *Zoölogy.* World Book Co., 1920.

Conklin, E. G. *Heredity and Environment in the Development of Men.* 4th edition. Princeton University Press, 1922.

Conklin, E. G. *The Direction of Human Evolution.* Charles Scribner's Sons, 1921.

Creation by Evolution (Mason, Ed.) (A consensus of present-day knowledge of evolution as set forth by twenty-five scientists.) The Macmillan Co., 1928.

Curtis, W. C., and Guthrie, M. J. *Textbook of General Zoölogy.* 2d edition. John Wiley and Sons.

Dahlgren, Ulric, and Kepner, W. A. *Principles of Animal Histology.* The Macmillan Co., 1908.

Darwin, Charles. *The Origin of Species.* London, 1859. 6th edition, 1880.

Darwin, Charles. *The Descent of Man.* London, 1871.

Darwin, Charles. *Variation in Animals and Plants under Domestication.* London, 1868.

Dendy, Arthur. *Outlines of Evolutionary Biology.* D. Appleton & Co., 1911.

DREW, G. A. *Invertebrate Zoölogy.* 3d edition. W. B. Saunders Co., 1920.

GEDDES, P., and THOMSON, J. A. *Sex.* Henry Holt & Co., 1914.

GUYER, M. F. *Animal Micrology.* 2d edition. The University of Chicago Press, 1917.

GUYER, M. F. *Animal Biology.* Harper and Bros., 1931.

GUYER, M. F. *Being Well-Born.* Revised edition. Bobbs-Merrill Co., 1925.

HEGNER, R. W. *An Introduction to Zoölogy.* The Macmillan Co., 1910.

HEGNER, R. W. *College Zoölogy.* Revised edition. The Macmillan Co., 1926.

HEGNER, R. W. *The Germ-Cell Cycle in Animals.* The Macmillan Co., 1914.

HEGNER, R. W. *Practical Zoölogy.* The Macmillan Co., 1915.

HEGNER, R. W. *Invertebrate Zoölogy.* The Macmillan Co., 1933.

HENDERSON, L. J. *The Fitness of the Environment.* The Macmillan Co., 1913.

HERTWIG, R., and KINGSLEY, J. S. (translator). *A Manual of Zoölogy.* 3d edition. Henry Holt & Co., 1912.

HOLMES, S. J. *Biology of the Frog.* Revised edition. The Macmillan Co., 1925.

HOLMES, S. J. *The Trend of the Race.* Harcourt, Brace & Co., 1921.

HUXLEY, T. H. *Collected Essays.* D. Appleton & Co.

HYMAN, L. H. *A Laboratory Manual for Elementary Zoölogy.* The University of Chicago Press, 1919.

JENNINGS, H. S. *The Behavior of the Lower Organisms.* Columbia University Biological Series, 1906.

JENNINGS, H. S. *Life and Death, Heredity and Evolution in Unicellular Organisms.* Gorham Press, 1920.

JORDAN, D. S., and KELLOGG, V. L. *Evolution and Animal Life.* D. Appleton & Co., 1908.

KELLICOTT, W. E. *General Embryology.* Henry Holt & Co., 1913.

KELLOGG, V. L. *Darwinism Today.* Henry Holt & Co., 1908.

KINGSLEY, J. S. *Comparative Anatomy of Vertebrates.* 2d edition. P. Blakiston's Son & Co., 1917.

LANKESTER, E. R. (editor). *A Treatise on Zoölogy* (in 8 volumes). A. and C. Black, London.

LILLIE, F. R. "The Freemartin; A Study of the Action of Sex Hormones in the Foetal Life of Cattle." *Jour. Exp. Zoöl.*, Vol. 23, 1917.

LINSEY, A. W. *Problems of Evolution.* The Macmillan Co., 1931.

LOCY, W. A. *Biology and Its Makers.* 3d edition. Henry Holt & Co., 1915.

Locy, W. A. *The Main Currents of Zoölogy.* Henry Holt & Co., 1918.

Loeb, Jacques. *The Organism as a Whole.* New York, 1916.

Loeb, Jacques. *Forced Movements, Tropisms, and Animal Conduct.* J. B. Lippincott, 1919.

Lull, R. S. *Organic Evolution.* The Macmillan Co., 1917.

McFarland, J. *Biology, General and Medical.* 3d edition. W. B. Saunders Co., 1918.

Moore, B. *The Origin and Nature of Life.* Henry Holt & Co., 1912.

Morgan, T. H. *Evolution and Adaptation.* The Macmillan Co., 1903.

Morgan, T. H. *Heredity and Sex.* Columbia University Press, 1913.

Morgan, T. H. *The Physical Basis of Heredity.* J. B. Lippincott & Co., 1919.

Newman, H. H. *Vertebrate Zoölogy.* The Macmillan Co., 1920.

Newman, H. H. *Readings in Evolution, Genetics and Eugenics.* 3d edition. The University of Chicago Press, 1932.

Newman, H. H. *The Biology of Twins.* The University of Chicago Press, 1917.

Newman, H. H. *The Physiology of Twinning.* The University of Chicago Press, 1923.

Newman, H. H. *Evolution Yesterday and Today.* Williams and Wilkins Co., 1932.

Newman, H. H., and others. *The Nature of the World and of Man.* The University of Chicago Press, 1926.

Nuttall, G. H. P. *Blood Immunity and Blood Relationship.* London, 1904.

Osborn, H. F. *From the Greeks to Darwin.* The Macmillan Co., 1894.

Osborn, H. F. *The Origin and Evolution of Life.* Charles Scribner's Sons, 1917.

Parker, T. J., and Haswell, W. A. *Textbook of Zoölogy.* 3d edition. The Macmillan Co., 1922.

Plunkett, C. R. *Elements of Modern Biology.* Henry Holt & Co., 1934.

Ritter, W. E. *The Unity of the Organism.* Richard G. Badger, 1919.

Romer, A. S. *Man and the Vertebrates.* The University of Chicago Press, 1933.

Scott, W. B. *The Theory of Evolution.* The Macmillan Co., 1917.

Sedgwick, W. T., and Wilson, E. B. *General Biology.* Henry Holt & Co., 1895.

Sharp, L. W. *Introduction to Cytology.* McGraw-Hill Book Co., 1921.

Shelford, V. E. *Animal Communities in Temperate America.* The University of Chicago Press, 1913.

Shipley, A. E., and MacBride, E. W. *Zoölogy.* The Macmillan Co., 1901.

Shull, A. F., *et al.* *Principles of Animal Biology.* 4th edition. McGraw-Hill Book Co., 1934.

Snodgrass, R. E. *The Anatomy and Physiology of the Honey Bee.* McGraw-Hill Book Co., 1925.

Thomson, J. A. *Darwinism and Human Life.* Henry Holt & Co., 1908.

Verworn, Max. *General Physiology.* The Macmillan Co., 1899.

Walter, H. E. *Genetics.* The Macmillan Co., 1922.

Ward, H. B., and Whipple, G. C. *Fresh-Water Biology.* John Wiley & Sons, 1918.

Weismann, A. *The Germ Plasm.* Charles Scribner's Sons, 1892.

Wells, H. G., Huxley, J. S., and Wells, G. P. *The Science of Life.* Doubleday, Doran & Co., 1931.

Whitman, C. O. "The Inadequacy of the Cell Theory." *Woods Hole Biological Lectures*, 1893.

Wilson, E. B. *The Cell in Development and Heredity.* 3d edition. The Macmillan Co., 1925.

Wilson, E. B. "The Problem of Development." *Science*, N. S., 1905.

Woodruff, L. L. *Foundations of Biology.* 5th edition. The Macmillan Co., 1936.

GLOSSARY

ABIOGENESIS. The abandoned doctrine that living organisms or living matter may or does arise from nonliving matter; same as SPONTANEOUS GENERATION.

ABORAL. Opposite the mouth.

ABORTIVE. Unsuccessful; incapable of functioning.

ACCLIMATION. The process of becoming habituated to environmental conditions not native.

ACHROMATIC FIGURE. That part of the mitotic figure that does not stain deeply, namely, the spindle together with the central body and asters.

ACŒLOMATA. A group of animal phyla characterized by the absence of a cœlom.

ACTINIC RAYS. The chemically active rays of sunlight or other lights.

ADAPTATION. The mutual fitness of organism and environment; a structure or reaction fitted for a particular feature of the environment or for a particular function in the body; the process of becoming fitted to an environment.

ADDUCTOR. One of the large muscles attached to the valves of a mussel shell, by means of which the shell is closed; any muscle which draws a structure toward the median axis; referring to any muscle that moves a part toward the body.

ADIPOSE. Pertaining to fat.

ADRENALIN. The specific enzyme secreted by the suprarenal (adrenal) glands.

AFFERENT NERVE. Any nerve that conducts impulses from the peripheral sense organs to the central nervous system.

ALGÆ. A large and heterogeneous group of lower plants in which the body is unicellular or consists of a thallus.

ALIMENTARY. Pertaining to digestion or to the digestive tract.

ALLANTOIS. An embryonic membrane of land vertebrates, used primarily for embryonic respiration.

ALLELOMORPHS. Genes similarly situated on homologous chromosomes which produce alternative or contrasting characters.

ALTERNATION OF GENERATIONS. See METAGENESIS.

ALVEOLAR. Of the nature of an emulsion.

ALVEOLUS. One of the separate droplets of an emulsion. Also one of the ultimate air spaces of the lung.

AMBULACRAL. Literally, resembling an alley; a term applied to the grooves on the oral surface of echinoderms in which are found the tube feet.

AMBULATORY. Pertaining to walking.

AMINO-ACID. One of a number of organic acids in which one hydrogen ion is replaced by the amino radical (NH_2). These acids are known as the building stones of proteins.

AMITOSIS. Cell division not involving the formation of discrete chromosomes or a spindle; direct cell division.

AMNION. A thin membrane surrounding the embryos of reptiles, birds, and mammals.

AMŒBOID. Usually applied to cell movements resembling those in Amœba; movement by means of pseudopodia.

AMPHIASTER. The figure produced by the two asters and the spindle in the dividing cell.

AMPHIBIA. A class of vertebrates including frogs, toads, newts, salamanders, etc.

AMPULLA. The flask-shaped bulb associated with the movement of the tube feet of echinoderms. Also, a bulbous enlargement at the base of a semicircular canal in which lie the sense cells of equilibration.

AMYLOPSIN. A starch-digesting enzyme produced by the pancreas.

ANABOLISM. The constructive phase of metabolism.

ANAL. Pertaining to the anus.

ANALOGOUS. Similar in function but not homologous.

ANAPHASE. All stages of mitosis during which the chromosomes, after longitudinal division, are passing from the equatorial plate of the spindle to the ends of the latter.

ANATOMY. The science which treats of the structure of animals; especially that which may be made out by dissection.

ANIMAL POLE. That part of an egg in which the protoplasm is concentrated, which has the highest rate of metabolism, and which in most organisms goes to form the nervous system and sense organs.

ANISOGAMY. The condition of having gametes somewhat differentiated, but not fully specialized as eggs and sperms. See ISOGAMY.

ANNELID. A member of the Phylum Annelida, the segmented worms.

ANTENNA. One of a pair of jointed appendages belonging to an arthropod, usually sensory in function.

ANTERIOR. Pertaining to the front or head end of animals with an axis of polarity. In human anatomy, the ventral side.

ANTHROPOID. Manlike. Referring especially to manlike apes.

ANUS. The posterior opening of the alimentary tract.

AORTA. A large trunk artery carrying blood away from the heart.

AORTIC ARCHES. Arteries arising from the ventral aorta and supplying the gills in aquatic vertebrates; also found in the embryos of the higher (terrestrial) vertebrates.

Aphids. Small sucking insects, commonly called "Plant Lice" and usually green in color.

Apical. Pertaining to that part of the axis of an axiate organism which has the highest rate of metabolism and exercises a dominance or control over other parts of the axis.

Appendicular Skeleton. That part of the skeleton of a vertebrate which consists of the limbs and the limb girdles.

Archenteron. The primitive digestive tract of a gastrula. The primitive gut.

Aristotle's Lantern. The elaborate masticatory apparatus of a sea urchin.

Armadillo. An armored mammal belonging to the order Edentata.

Artery. A blood vessel conducting blood from the heart.

Arthropod. An animal belonging to the Phylum Arthropoda, which includes Crustacea, Arachnida, Myriapoda, and Insecta.

Artificial Parthenogenesis. The artificial activation of an egg to develop without fertilization.

Asexual. Sexless. Without the use of gametes.

Assimilation. The conversion of digested foods and other materials into protoplasmic substances.

Aster. The starlike figure composed of the central body and the radiations from it; or the central body may be absent.

Asymmetry. Absence of symmetry; more particularly, the development on one side of a bilateral organism of structures not present on the opposite side. An aberration of bilateral symmetry.

Atlas. The first vertebra on which the skull rests.

Atoms. The elementary particles of matter that enter into chemical reactions. The "fundamental" units of matter.

Attraction Sphere. A differentiated portion of the cytoplasm, usually lying near the nucleus, and usually containing a central body. The whole structure is associated with mitotic cell division.

Auditory. Pertaining to the sense of hearing.

Auricle. The anterior chamber of the heart of fishes, and one of the two anterior chambers in that of higher vertebrates. Also the lateral sense organs on the side of the head of a flatworm.

Autosome. Any one of the chromosomes of a cell except the X- or the Y-chromosome.

Autotomy. Self-mutilation, as in the voluntary cutting off of the arm of a starfish or the chela of a lobster.

Aves. The class of vertebrates consisting of birds.

Avoiding Reaction. The more or less stereotyped protective reflex induced in an organism by an adverse stimulus.

Axial Gradient. The orderly arrangement of regions of differing metabolic rate in which the apical end has the highest rate and there is a steady decrease in rate as one proceeds from apical to basal levels of the axis. The name of a theory of organic individuation.

Axial Skeleton. That part of the skeleton of a vertebrate consisting of the cranium and the spinal column.

Axis of Polarity. An imaginary line running from the anterior to the posterior end of an organism.

Axis of Symmetry. Double or twin metabolic gradients running from the mid-dorsal (mid-ventral in invertebrates) region laterally and ventrally (dorsally in invertebrates).

Axolotl. The name applied to the neotenic larva of the tiger salamander, *Amblystoma tigrinum*, which reproduces in the larval state.

Axone. The projection from a nerve cell that usually conducts impulses away from the body of the cell.

Bacteria. Microscopic unicellular plants, some of which are responsible for diseases in host organisms and others for the decay or decomposition of organic matter.

Barnacle. A kind of degenerate sessile crustacean, usually covered by a hard shell and found on rocks, piles, and ship bottoms.

Basement Membrane. A thin layer of noncellular material separating the ectoderm from the endoderm in Hydra and its relatives.

Bilateral Symmetry. An arrangement of the parts of an organism such that the halves on opposite sides of a sagittal plane are mirror images of each other.

Bile. The fluid secreted by the liver in vertebrates.

Bile Duct. The tube through which the bile is discharged into the intestine.

Bilobed. Divided into two lobes or segments.

Binary Fission. The division of a cell, especially of a unicellular organism, into two daughter cells.

Binomial Nomenclature. The accepted scientific method of naming species of organisms by two Latin or Latinized words, the first designating the genus and the second the species. E.g., the dog, *Canis familiaris*.

Biology. The branch of science that deals with living organisms, both animals and plants; more technically, the study of the manifestations of matter in the living state.

Biophysics. The study of the physical aspects of biology.

Biparental. Derived from two parents, male and female.

Biradial Symmetry. A modified form of radial symmetry in which the radii are arranged in two sets that are mirror images of each other. An incipient form of bilateral symmetry.

Bisexual. Having both sexes. See Hermaphrodite.

BLADDER WORM. One stage in the life cycle of the tapeworm.

BLASTOCŒLE. The cavity of the blastula.

BLASTOMERE. One of the cells produced by the early divisions (cleavage) of the egg.

BLASTOPORE. The opening through which the cavity of the gastrula communicates with the exterior.

BLASTULA. An early developmental stage typically consisting of a hollow ball of cells.

BLOOD. A fluid tissue consisting of blood cells, or *corpuscles*, and a liquid intercellular material, the *plasma*.

BLOOD CORPUSCLE. A detached cell present in the fluid plasma of the blood. There are two principal kinds, red and white.

BOWMAN'S CAPSULE. The expanded end of the kidney tubule, in which a glomerulus is located.

BUCCAL CAVITY. Mouth cavity.

BUCCAL MASS. The complex of muscles, jaws, radula, and digestive glands making up the anterior part of the digestive tract in certain mollusks, such as the gastropods and cephalopods.

BUD. An undeveloped lateral branch of an organism, e.g., the bud of a Hydra, of a plant.

BUDDING. The division of an organism in such a way that the main part is left intact and the secondary part is relatively small and usually has an axis at right angles to the parent organism.

CÆCUM. A blind, saclike extension of the large intestine in vertebrates.

CALCAREOUS. Composed of salts of calcium or lime.

CALCIFEROUS GLANDS. Glands which are supposed to secrete calcium carbonate into the œsophagus of the earthworm, believed to serve the function of neutralizing the acidity of the food.

CALCIFIED CARTILAGE. Cartilage in which there is a deposit of salts of calcium.

CAMBRIAN. The name applied to one of the earliest of the geological periods and the earliest from which fossils have been taken.

CAMOUFLAGE. The art of concealment by the use of colors or patterns that deceive the eye.

CANALICULUS. One of the numerous minute channels radiating from a lacuna in bone, through which extend slender processes of the bone cells.

CAPILLARY. One of the ultimate branches of the blood vessels that carry blood directly to the tissues and cells of the body.

CARBOHYDRATE. Any one of a class of organic substances, such as sugars, starches, cellulose, etc., composed of carbon, hydrogen, and oxygen, and usually with two atoms of hydrogen to one of oxygen.

CARDIAC. Pertaining to the heart.

CARNIVOROUS. Flesh eating. See HERBIVOROUS.

CARTILAGE. A flexible, somewhat translucent tissue composed of cells embedded in a matrix.

CAST. A sort of fossil produced by a mass of rock forming in a mold left in soft mud by an organism.

CASTE. One of several distinct types of individuals of one species in a diversified animal community, such as that of ants or termites.

CATABOLISM. The breaking down or destructive phases of metabolism.

CATACLYSMIC THEORY. A doctrine held during the Middle Ages to the effect that the stratification of the earth, the formation of mountain ranges, etc., had come about as the result of a series of vast and violent disturbances that destroyed all existing animals and plants, necessitating repeated special creations to repeople the world.

CATALYST. Any substance which brings about or accelerates a chemical reaction without being used up in the process.

CAUDAL. Pertaining to the tail, or near the tail.

CELL. A small mass of protoplasm containing a nucleus or nuclear material. A fundamental life unit.

CELL MEMBRANE. A specialized surface layer of protoplasm surrounding a cell. Plasma membrane.

CELL THEORY. The theory that all animals and plants consist of similar units called cells. According to this theory a protozoan organism is equivalent to a tissue cell of a metazoan organism.

CELL WALL. A nonliving structure secreted by the surface protoplasm of a cell, and commonly composed of cellulose or chitin.

CELLULOSE. A substance, one of the carbohydrates, out of which the walls of plant cells are composed.

CENOZOIC. Pertaining to the most recent geologic era. The age of mammals.

CENTIPEDE. A member of the Class Myriapoda, Phylum Arthropoda.

CENTRAL BODY. That structure which forms the focus of the aster in mitotic cell division. An older term for this structure is CENTROSOME.

CENTRAL NERVOUS SYSTEM. The brain and spinal cord; the principal ganglia and their connectives.

CENTROSOME. See CENTRAL BODY.

CENTROSPHERE. Same as ATTRACTION SPHERE.

CEPHALIC. Pertaining to the head.

CEPHALIZATION. The process of head formation. More particularly, the evolution of the larger and more elaborate brain and head of the higher organisms from the smaller and less specialized head of lower forms.

CEPHALOPOD. A member of the Class Cephalopoda, of the Phylum Mollusca.

Cercaria. The tailed larval form of the liver fluke, Fasciola, and allied forms.

Cerebellum. A division of the brain in the vertebrates developed from the dorsal side anterior to the medulla oblongata.

Cerebral. Pertaining to the Cerebrum.

Cerebrum. The anterior portion of the brain in vertebrates; in man, the main bulk of the brain.

Chætæ. Spines or bristles imbedded in the body wall or in the parapodia of the annelids.

Cheliped. The fourth thoracic appendage in the crayfish and its allies; usually in the form of a pincher.

Chemotropism. The response of an organism to chemical stimuli.

Chitin. A horny substance forming the exoskeleton of insects and other arthropods.

Chitinous. Composed of chitin.

Chiton. A genus of primitive mollusks, having a longitudinal series of eight dorsal shells.

Chloragogue Cells. The cells of the outer layer of the intestine in the earthworm.

Chlorophyll. The green pigment which catalyzes photosynthesis.

Chloroplast. A cellular organelle (plastid) containing chlorophyll.

Chondrocranium. A skull or cranium composed of cartilage; found in adult sharks and in the embryos of higher vertebrates.

Chordate. Pertaining to the Phylum Chordata. A member of the Phylum Chordata.

Chromatin. A deeply staining protoplasmic substance characteristic of the nucleus, forming chromosomes, etc.

Chromomere. One of the beadlike granules that are arranged in a chain or linear series to form a chromosome.

Chromosome. One of the deeply staining rodlike or rounded bodies into which the chromatin network resolves itself during mitosis.

Cilia. Delicate whiplike protoplasmic projections from the surface of a cell, used either as organs of locomotion or as a means of transporting substances in ducts or passages.

Ciliate. Provided with cilia; pertaining to the Class Ciliata; a member of the protozoan Class Infusoria. Same as Ciliated.

Circulation. The movement of blood through the system of blood vessels.

Circulatory. Referring to organs of circulation.

Cirri. Soft tentacle-like projections or appendages.

Class. A division of a phylum; a group superior in rank to an order.

Cleavage. The mitotic division of an egg to form blastomeres.

Cleavage Cavity. Same as Blastocœle or Segmentation Cavity.

Clitellum. A thickened glandular region of the body wall of the earthworm and other annelids, used in the formation of the cocoon.

Cloaca. A common passageway or vestibule into which the intestine, the kidneys, and the sexual organs discharge their products; present in some fishes, in amphibia, in reptiles, in birds, and in some of the primitive mammals.

Cnidoblast. A type of formative cell which, in the Cœlenterata, forms a nematocyst.

Cnidocil. The delicate sensory projection or "trigger" of a nematocyst.

Cochlea. The spirally coiled portion of the membranous labyrinth of the inner ear of higher vertebrates in which lie the auditory sense cells and their accessories.

Cocoon. A sac or case in which eggs are stored and in which larvæ develop; also the silky covering around a pupa.

Cœlenterate. Pertaining to the Phylum Cœlenterata; a member of this phylum.

Cœlom. The true body cavity, lying between the digestive tract and the body wall; lined with and formed from mesodermal tissue.

Cœlomata. A large group of animal phyla characterized by having a cœlom.

Cœlomate. Pertaining to the cœlom; any member of the Animal Kingdom possessing a cœlom. All animals without a cœlom are referred to as Acœlomate.

Colloid. A state of matter in which particles larger than molecules are held in suspension or solution in a fluid or semifluid medium.

Colloidal. Pertaining to a colloid.

Colony. A group of individuals of the same species organically connected with one another. These sometimes are so closely integrated as almost to form a superior unit or individual.

Columnar Epithelium. A type of epithelial tissue in which the individual cells are somewhat elongated or column-shaped, and have their greater axis at right angles to the surface.

Combination. A type of genetic variation due to the recombination of genes during maturation or fertilization.

Combustion. The oxidation of chemical substances, usually accompanied by a release of heat or some other form of energy.

Commensalism. The association of members of two or more species in which neither may be strictly parasitic upon the other in the sense that one feeds upon the tissues of its associate.

Commissure. A bundle of nerve fibers connecting two ganglia.

Conditioned Reflex. A habitual response to a particular stimulus determined by the previous experience of the individual.

Conjugation. A temporary union of two protozoa during which nuclear exchanges take place; the sexual phase in the life cycle of Infusoria.

Connective Tissue. A tissue composed of cells and materials excreted by cells, which in its simpler forms binds other tissues or organs together. In its broader sense it includes cartilage, bone, adipose tissue, tendons, and ligaments.

Contractile Vacuole. A vesicular reservoir in Protozoa in which water and waste products collect and are discharged to the outside by means of a contraction of the vacuole. Same as Pulsating Vacuole.

Conus Arteriosus. A portion of the circulatory system of vertebrates lying between the heart (ventricle) and the aortic arches.

Coördination. The production of harmonious interaction of the various parts and processes in an organism.

Copulation. The sexual union of two individuals, during which spermatozoa are introduced into the oviduct of the female.

Coracoid. A bone found in the pectoral girdle of most vertebrates.

Cortex. A name sometimes applied to the layer of the ectoplasm beneath the cuticle in Paramecium and its allies. More generally, any layer just beneath the surface layer.

Cosmos. The whole organized universe.

Cranial Nerves. Nerves that arise from the brain.

Cranium. Same as Skull. The bony or cartilaginous case that incloses or partly incloses the brain.

Cretin. A defective (subnormal) type of animal or human being, resulting from either congenital or operative deficiency of thyroid secretion.

Crinoid. A member of the Class Crinoidea of the Phylum Echinodermata, commonly known as sea lilies.

Crossing Over. The rearranging of linked characters as the result of exchanges of genes between homologous chromosomes during synapsis.

Crustacean. Pertaining to the Class Crustacea of the Phylum Arthropoda. A member of this class.

Crystalloid. A substance which so dissolves in a solute that extremely small particles, small molecules, or ions, evenly diffuse throughout the medium.

Cuticle. A surface layer of cells or a noncellular layer; more particularly, the dead surface cells of the epidermis.

Cuttlefish. A kind of cephalopod mollusk related to the squid and the octopus.

Cypris Larva. The characteristic larva of the order Cirripedia of the Class Crustacea. Seen in the barnacles and in Sacculina.

Cyst. A small capsule or sac.

Cysticercus. The bladder-worm stage in the life cycle of the tapeworm.

Cytogenic Reproduction. That type of reproduction that is effected by means of single reproductive cells, which by growth and division

give rise to a new multicellular body. In contrast with SOMATOGENIC REPRODUCTION.

CYTOLOGY. The science which deals with the structure and function of cells, especially of germ cells.

CYTOPLASM. The protoplasmic material of which the cytosome consists. Formerly used in same sense as CYTOSOME.

CYTOPLASMIC INCLUSIONS. Any materials not strictly living that lie in the cytoplasm.

CYTOSOME. That part of the cell that lies outside the nucleus. An older term for this is CYTOPLASM.

DARWINISM. The theory of Natural Selection, proposed by Charles Darwin. Wrongly used as a synonym for EVOLUTION.

DE NOVO. A common Latin expression used in biology to indicate an origin from no known source or from no similar structure.

DENDRITE. A projection from the body of a nerve cell which ordinarily conducts impulses toward the body of the cell.

DENITRIFYING BACTERIA. Bacteria which decompose nitrogen compounds and release free oxygen into the atmosphere.

DERMAL. Pertaining to or arising from the DERMIS.

DERMIS. The deeper skin beneath the EPIDERMIS.

DETERMINATE CLEAVAGE. The early divisions of an egg in which each blastomere can be traced to some prospective organ or tissue and in which the cells from the first are arranged with reference to the prospective axes of the organism.

DETERMINER. Same as GENE.

DIAPHRAGM. A muscular partition between the thoracic and abdominal cavities in mammals.

DIFFERENTIATION. A process of becoming structurally or functionally unlike the original condition. Similar to SPECIALIZATION.

DIFFUSION. The spreading of molecules of one substance among those of another.

DIGESTION. The conversion of food into soluble substances which may diffuse through the tissues and into the protoplasm.

DIHYBRID. The offspring of parents differing with regard to two given characters. A kind of cross involving two different pairs of genes.

DIŒCIOUS. Having the male and female organs in separate individuals. The opposite of MONŒCIOUS.

DIPHYLETIC TREE. A schematic representation of the supposed ancestral relations of the various animal phyla. The tree has a short common trunk and two main branches.

DIPLOBLASTIC. Composed of two fundamentally different layers of cells, ectoderm and endoderm.

DIPLOID. The maximum or full (duplex) number of chromosomes, found in body cells (soma) and in the unmaturated germ cells. See HAPLOID.

DIRECT CELL DIVISION. Same as AMITOSIS.

DISSEPIMENT. A thin partition, derived from the segmental cœloms, between two adjacent cœloms in annelid worms. Same as SEPTA.

DIZYGOTIC. Derived from two eggs, or zygotes. Said of certain kinds of twins. See MONOZYGOTIC.

DOMINANT CHARACTER. One of a pair of alternative characters which appears to the exclusion of the other in the F_1 generation in Mendelian heredity.

DORSAL. Pertaining to the back; hence, usually, upper.

DORSAL AORTA. The chief artery distributing pure blood to the body.

DUCTLESS GLAND. See ENDOCRINE GLAND.

DUODENUM. The anterior of the three divisions of the small intestine.

ECDYSIS. The shedding of the exoskeleton in the Arthropoda.

ECHINODERM. A member of the Phylum Echinodermata. Pertaining to the latter.

ECOLOGY. That branch of biology dealing with the relation of organisms to their environment.

ECTODERM. The outer layer of cells of the gastrula stage of development; the cellular derivatives of this layer in later stages of development.

ECTODERMAL. Derived from or pertaining to the ECTODERM.

ECTOPLASM. The outer layer of protoplasm in a protozoan organism. Sometimes called ECTOSARC.

EFFECTOR. A structure specialized for the production of some particular kind of response such as movement or secretion.

EFFERENT NERVE FIBER. A fiber carrying impulses away from the central nervous system toward the periphery or toward an organ; a nerve fiber carrying motor impulses.

EGESTION. The elimination of solid waste material from the cell or from the digestive tract.

EGG. A female germ cell after the process of maturation has been completed. Same as OÖTID.

ELECTROLITE. A substance whose molecules dissociate into ions.

ELECTRON. A particle of negative electricity, one of the ultimate constituents of matter. See PROTON.

ELEMENT. A substance containing only one kind of atoms.

ELEMENTAL THEORY. The doctrine that the whole or the individual is to be fully explained as the result of the summation of the characteristics and activities of its ultimate parts. To be contrasted with the ORGANISMAL THEORY.

EMBRYO. An undeveloped organism while still within the egg membrane and nourished by the substances stored in the egg or by nutritive materials derived from the uterus. To be contrasted with LARVA.

EMBRYOLOGY. The science which deals with the development of the embryo.

EMBRYONIC. Pertaining to an embryo.

EMERGENT EVOLUTION THEORY. A theory that when lesser units are combined to form greater units, which become organized into a new whole, new properties of the whole emerge that are more than the sum of the properties of the parts.

EMULSION. A dispersion consisting of small droplets of one liquid in another.

ENCYSTMENT. The process of becoming inclosed in an impermeable envelope or CYST.

ENDOCRINE GLAND. A gland whose secretion passes directly from the cells into the blood stream without passing through ducts. Sometimes called DUCTLESS GLAND.

ENDODERM. The inner layer of cells of the gastrula; or the derivatives of this layer in later stages.

ENDOMYXIS. A nuclear reorganization in Protozoa, e.g., Paramecium, which does not involve conjugation or the exchange of nuclear materials between different individuals. Similar to PARTHENOGENESIS in Metazoa.

ENDOPLASM. The inner mass of protoplasm in cells, particularly the Protozoa, in which the outer layer is differentiated into an ECTOPLASM.

ENDOPODITE. The inner of the two distal parts of the typical biramous crustacean appendage.

ENDOTHELIUM. A layer of cells of endodermal origin lining the passages of the alimentary tract and its derivatives.

ENERGY. The capacity to do work; i.e., to produce a change.

ENTOMOLOGY. That branch of Zoölogy that deals with the study of insects.

ENZYME. An organic substance which brings about or hastens a chemical reaction but is not consumed in the process. Usually secreted by glands. An organic catalyst.

EPIDERMIS. The outer layer of the skin, derived from the ectoderm.

EPIGENESIS. The doctrine that the germ cell is absolutely, or relatively structureless and that differentiation arises *de novo* through the interaction of the protoplasm and the environment. To be contrasted with PREFORMATION.

EPITHELIAL. Pertaining to an epithelium.

EPITHELIUM. A layer of cells at the outer or inner surface of an organ or passage.

EQUATORIAL PLATE. The flattened group of chromosomes at the equator of the spindle in a dividing cell.

EREPSIN. An enzyme secreted by the intestine, which splits up peptones into amino-acids.

EROSION. The wearing away of rock or soil through the action of water or other agencies.

EUGENICS. The science which applies the principles of genetics for the purpose of race improvement. See EUTHENICS.

EUSTACHIAN TUBE. A passage in air-breathing vertebrates, connecting the pharynx with the middle ear. A survival of the first gill slit of the embryo.

EUTHENICS. The science dealing with the improvement of the human race by improving the environment. See EUGENICS.

EVAGINATION. The folding of a layer of cells outward from an inclosed cavity. See INVAGINATION.

EVISCERATE. To remove or cast out the internal organs from the body cavity.

EVOLUTION, ORGANIC. The theory that animals and plants have undergone gradual changes through the process of descent with modification, and that the species of today have been derived from those of the past. The antithesis of the doctrine of SPECIAL CREATION.

EXCRETION. The process of elimination of the dissolved waste products of metabolism. The waste products themselves.

EXCRETORY. Pertaining to excretion.

EXCURRENT. An excurrent canal, pore, siphon, or other structure is one that conducts water or other fluid away from an individual, organ, or cavity. Opposite to INCURRENT.

EXOPODITE. The outer of the terminal segments of a typical biramous crustacean appendage. See ENDOPODITE.

EYE-SPOT. A light-sensitive pigmented area connected with the central nervous system and playing the rôle of a simple eye.

F_1. An individual or generation of individuals resulting from the crossing of two unlike parents. An abbreviation for *first filial.*

F_2. An individual or generation of individuals resulting from the intermating of individuals of the F_1 generations. An abbreviation for *second filial.*

F_3. An individual or generation of individuals resulting from the intermating of the individuals of the F_2 generation.

FACTOR. An agent or agency influencing the development of an individual or the evolution of a race. In genetics, the same as a GENE. One of several interacting elements in a complex process.

FAMILY. A taxonomic group of higher rank than a genus but below an order.

Fats. One of the chief groups of foodstuffs; one of the ingredients of protoplasm. A compound of glycerol and one or more fatty acids.

Fatty Acid. One of a group of organic acids, such as acetic, butyric, and stearic acids.

Fauna. The animals of any given geographic area or geological period.

Faunistic. Pertaining to faunas.

Fertilization. The union of the egg with the spermatozoön. More broadly, the union of a pair of gametes.

Fetus. An advanced embryo of a mammal. Same as Fœtus.

Fibril. A very slender fiber. More particularly, one of the longitudinal contractile threads of a voluntary muscle fiber.

Fibrillar. Pertaining to fibrils; composed of fibrils.

Filterable Viruses. Ultramicroscopic living units parasitic within the cells of other organisms.

Fission. The division of an organism into two approximately equal parts. More generally, division of any sort that involves the cutting off of any part of an organism already formed, in order to produce two individuals or two organs.

Flagellate. Possessing flagella; pertaining to flagella. As a noun, a member of the Class Mastigophora of the Subkingdom Protozoa.

Flagellum (pl. Flagella). A long whiplike motile projection from a cell.

Flame Cell. A cell with a hollow interior in which there is a bunch of vibratile cilia; part of the excretory apparatus of the flatworms.

Flatworm. One of the members of the Phylum Platyhelminthes.

Fluctuations. Somatic variations resulting from differences in environment or in function, and not hereditary.

Fluke. A parasitic flatworm belonging to the Class Trematoda.

Food. Any material that yields energy for the activities of an organism.

Foot. Technically, the basal muscular part of a mollusk. More generally, the terminal part of a leg, the basal disk of a Hydra, etc.

Formative Cell. One of the undifferentiated cells of the ectoderm of a Hydra.

Fossil. The preserved remains or other indication of a prehistoric organism.

Freemartin. The partially masculinized female member of a pair of cattle twins.

Galaxy. A vast organized unit of the cosmos, composed of millions of star-suns.

Gall Bladder. A saclike receptacle in the liver for storing bile.

Galvanotropism. The response of an organism to an electric current.

Gamete. A cell which unites with another cell in sexual reproduction.

Ganglion. An aggregate of nerve cells.

GASTRIC. Pertaining to the stomach.

GASTRIN. A hormone secreted by the cells lining the stomach which stimulates the gastric glands to secrete gastric juice.

GASTROVASCULAR. Serving the double function of digestion and circulation.

GASTRULA. A stage in the development of metazoan animals in which the embryo typically consists of a two-layered sac, with an archenteron, or primitive intestine, and a single opening, the blastopore.

GASTRULATION. The process of invaginating or infolding the vegetal-pole cells of the blastula into the blastocœle. The process of forming a gastrula.

GEL. A mixture of solid or semisolid consistency containing a large proportion of its liquid entrapped in the meshes of its solid component. One of the two alternative phases of a colloid. See SOL.

GELATINE. A colloidal substance obtained by boiling cartilage, bone, etc.

GEMMULE. A reproductive body composed of a number of cells, in sponges.

GENE. A factor or element in the chromosomes of germ cells or other cells which conditions a character of an organism.

GENETICS. Experimental evolution. The science of variation, heredity, sex biology, etc.

GENITAL. Pertaining to, or concerned with, reproduction.

GENOTYPE. The genetic constitution of an organism, or a group of genetically identical organisms.

GENOTYPIC. Pertaining to the germinal or hereditary constitution of an organism. See PHENOTYPIC.

GENUS. A taxonomic division composed of two or more species that have a large number of characters in common and are therefore believed to have been derived from a common ancestor. A main division of a family.

GERM CELLS. Cells capable of reproducing the organism.

GERMINAL CONTINUITY. The concept of an unbroken stream of germ plasm from generation to generation back to the beginning of life.

GERM LAYER. A primary embryonic tissue, such as ectoderm, endoderm, mesoderm, from which the tissues and organs of an organism develop.

GERM PLASM. The specific hereditary material forming the bridge between successive generations. More particularly, the chromatin of germ cells. In contrast with SOMATOPLASM.

GILL BOOK. A type of external respiratory organ found in aquatic Arachnida, composed of a series of leaves bound together by one edge and free elsewhere.

GILL SLIT. One of the openings connecting the pharynx with the outside; found in chordates. Also called GILL CLEFT or PHARYNGEAL CLEFT.

GLAND. An organ which secretes or excretes some special substance.

Glochidium. A bivalve larva of clams or their relatives, which commonly lives for some time parasitically imbedded in the gill tissues of fishes.

Glomerulus. A coil of capillaries at the end of each nephric tubule in the kidneys of the higher vertebrates.

Glottis. A slitlike opening in the pharynx leading to the trachea.

Glycerol. One of the alcohols. It enters into the composition of fats. Same as glycerin.

Glycogen. Animal starch. A common form of stored carbohydrate food in animal tissues.

Gonad. The organ (ovary or testis) in which germ cells are produced or lodged.

Gonophore. An individual which bears gonads or reproductive organs, as in Hydroids.

Gullet. Same as Œsophagus.

Gustatory. Referring to the sense of taste.

Habitat. The environmental complex in which an organism lives.

Hæmocœle. A specialized part of the cœlom or body cavity used as a blood channel or reservoir.

Hæmoglobin. The red coloring matter of the blood.

Haploid. The reduced (one half) number of chromosomes present in gametes. See Diploid.

Heliotropism. The response of organism to the direction of light.

Hepatic. Pertaining to the liver.

Herbivorous. Plant-eating. See Carnivorous.

Heredity. Organic resemblance based on descent. The transmission of genes from ancestors to descendants through the germ cells.

Hermaphrodite. An individual organism possessing both ovaries and testes.

Hermaphroditism. The state of being hermaphroditic. Same as Monœcious.

Heterogamy. The union of unlike gametes, as that of eggs and sperm.

Heteronomous. Having most of the metameres specialized in different ways. See Homonomous.

Heterozygous. Producing gametes which fall into equally numerous classes with respect to the genes (allelomorphs) for a pair of alternative characters. See Homozygous.

Hibernate. To pass the winter. Usually to go into a dormant state during the winter.

Histology. The science which deals with the structure and function of tissues.

Homology. Fundamental structural resemblance based on inheritance, and often modified to subserve a variety of functions.

HOMONOMOUS. Having most of the metameres in a segmental organism essentially alike. See HETERONOMOUS.

HOMOZYGOUS. Producing gametes that are all alike with respect to any given pair of alternative genes or allelomorphs. See HETEROZYGOUS.

HORMONE. An internal secretion, usually from a ductless gland, that circulates in the blood and acts as a stimulus to other organs or to growth processes.

HOST. An organism that harbors a parasite.

HUMERUS. The upper arm bone of the terrestrial vertebrates.

HYALINE. Glassy or semitransparent.

HYBRID. The offspring of two parents unlike in some heritable character.

HYDRA. A small tubular fresh-water cœlenterate with a crown of tentacles.

HYDROCŒLE. A specialized portion of the cœlomic system of an echinoderm larva, from which arises the radial water canals and which is responsible for the radial symmetry of the adult.

HYDROID. A colonial cœlenterate, the individuals of which resemble a Hydra.

HYDROLYSIS. Chemical decomposition of a substance by combining with water.

HYMENOPTERA. An order of insects comprising the bees, wasps, ants, etc.

HYOID. A group of bones or cartilages located at the base of the tongue.

HYPERTONIC. Possessing greater osmotic pressure than some other solution, e.g., sea water or blood, with which it is being compared.

HYPNOSIS. A form of sleep or somnambulism brought about by artificial means, in which there is usually suspension of some powers and unusual activity of others.

HYPOSTOME. The crater-like elevation about the mouth in Hydra.

HYPOTONIC. Possessing lower osmotic pressure than some other solution with which it is compared. See HYPERTONIC.

ILEUM. The last and usually the longest of the three divisions of the small intestine.

ILIUM. The dorsal bone of the pelvic girdle in the amphibia and higher vertebrates.

IMMUNITY. Resistance of an organism to disease-producing organisms.

INCURRENT. An incurrent canal, pore, siphon, or other structure is one that conducts water or other fluid toward or into an individual, organ, or cavity. Opposite of EXCURRENT.

INDETERMINATE CLEAVAGE. Segmentation of the egg in which the prospective fate of the individual cells is not readily traced and in which there is no great specialization of the blastomeres.

INDIRECT CELL DIVISION. Same as MITOSIS.

INFUSORIA. A class of Protozoa, usually possessing cilia.

INGESTION. The taking in of food.

INHIBITION. The stopping of some activity by a stimulus.

INSTINCT. An unconscious, stereotyped series of reflex actions, due to an inherited nervous pattern.

INSULIN. An internal secretion (hormone) of the pancreas essential to the normal metabolism of carbohydrates.

INTEGRATION. The process by means of which units of a lower order become united and correlated to form an individual of a higher order.

INTERCELLULAR. Between cells.

INTESTINE. That portion of the alimentary tract leading from the pyloric end of the stomach to the anus.

INTRACELLULAR. Within a cell.

INVAGINATION. The folding of a layer of cells inward into a cavity.

INVERTEBRATE. An animal without a backbone or vertebral column. See VERTEBRATE.

ION. A part of a molecule, composed of one or more atoms possessing an electric charge.

IRRITABILITY. Susceptibility to the influence of stimuli.

ISOGAMY. The union of like gametes. See HETEROGAMY.

ISOLATION. In genetics, the prevention of promiscuous interbreeding between a mutant or a new variety and the main body of the species.

ISOTONIC. Having the same osmotic pressure as another solution with which it is compared.

JEJUNUM. The second of the divisions of the small intestine.

JUGULAR VEIN. A large vein returning blood from the head.

KARYOKINESIS. Same as MITOSIS.

KERATIN. A substance forming the characteristic material of horn, hair, nails, hoofs, etc. Similar to CHITIN.

KIDNEY. The chief organ of excretion in vertebrates and in some invertebrates.

KINETIC ENERGY. Energy inherent in the motion of a body or its component parts.

KRAUSE'S MEMBRANE. A transverse partition of a voluntary muscle fiber.

LABIAL PALPS. Liplike, ciliated troughs leading into the mouth in many clamlike mollusks.

LABIUM. The lower lip in insects, as for example, the grasshopper.

LABRUM. The upper lip in insects.

LACUNA. A small space in the matrix of bone that, in life, contains a bone cell.

LAMARCKISM. The doctrine of the Inheritance of Acquired Characters.

LAMELLA. A thin layer.

LANCELET. A chordate belonging to the genus Amphioxus.

LANUGO. A coating of embryonic hair that appears in the human fetus at about the sixth month of pregnancy, covering the whole body except the palms and soles. It is lost before birth.

LARVA. An immature and more or less active stage in the development of an organism; with certain adaptive characters that have no prospective significance so far as adult structures are concerned.

LARYNX. The enlarged anterior end of the trachea, containing the vocal cords.

LENTICULAR. Pertaining to, or shaped like, a lens.

LEUCOCYTE. A white blood corpuscle.

LIGAMENT. A tough band of fibrous connective tissue attaching a muscle to a bone, or two muscles together.

LIGHT YEAR. An astronomical "measuring rod"; the distance light travels in a year going at a speed of about 186,000 miles per second.

LIMPET. A small type of gastropod mollusk with a simple noncoiled shell.

LININ. An achromatic substance that forms a network of threads in the nucleus.

LINKAGE. The tendency for certain characters to be inherited in groups, presumably because the genes for these characters occupy the same chromosome.

LIPIN. A kind of fat or fat-like substance.

LUMBAR. Referring to that part of the region of the spine of vertebrates back of the ribs.

LUNG BOOK. An inclosed respiratory organ composed of thin sheets of tissue bound together like the leaves of a book. Found in spiders and scorpions.

LYMPH. A clear fluid containing colorless cells found in lymph vessels. Essentially, blood without its solid constituents.

MACROGAMETE. The larger of the two kinds of gametes in species that exhibit heterogamy.

MACRONUCLEUS. The large nucleus in Infusoria, believed to be chiefly concerned with the vegetative activities of the cell.

MADREPORITE. The sievelike external opening of the water-vascular system in the echinoderms. Same as MADREPORIC PLATE.

MALARIA. A disease due to the presence of a sporozoan parasite in the red blood corpuscles.

MALPIGHIAN BODY. A structure in the vertebrate kidney composed of a combination of the Bowman's capsule and the glomerulus. Same as MALPIGHIAN CORPUSCLE.

MAMMAL. An animal belonging to the vertebrate Class Mammalia.

MAMMARY GLAND. The milk gland of a mammal.

MANDIBLE. A jaw. More particularly, the third pair of appendages of the head of the crayfish and its allies.

MANTLE. A specialized layer of tissue that secretes the shell in mollusks.

MARSUPIAL. A mammal having a pouch in which the young are carried.

MATRIX. The noncellular substance in which are imbedded the living cells of cartilage or bone.

MATTER. That which occupies space, has mass (inertia) and weight.

MATURATION. The process through which germ cells pass in preparation for fertilization, usually accompanied by a numerical reduction of chromosomes.

MAXILLA. One of the members of the fourth or fifth pair of head appendages of the crayfish and its allies.

MAXILLIPED. One of the members of any of the first three thoracic appendages of the crayfish and its allies.

MECHANISM. Any more or less complex groups of organs, systems, or minor parts of an organism that work in a regulated fashion and that subserve a useful function in preserving the life of the individual or the race. In order to be considered as a mechanism such a complex need not necessarily be wholly intelligible in terms of the physics and chemistry of lifeless materials.

MECHANISTIC VIEW. The view that life is explainable in terms of natural transformations of energy and of matter without introducing any immaterial or extra-natural "vital forces." This view is in distinct contrast with VITALISM.

MEDULLA OBLONGATA. The most posterior of the principal divisions of the vertebrate brain.

MEDULLARY PLATE, GROOVE, TUBE. Three phases or types of the central nervous system of vertebrates.

MEDULLARY SHEATH. A fatty insulating layer covering a nerve fiber or axone.

MEMBRANOUS LABYRINTH. The system of sacs and canals that make up the inner ear apparatus in vertebrates. It includes the sacculus, the utriculus, and the semicircular canals.

MERIDIONAL. In a plain parallel with the axis of polarity.

MESENTERY. A double sheet of tissue, continuous with the peritoneum, which supports an organ, such as an intestine, from the body wall.

MESODERM. The layer of cells between the ectoderm and the endoderm.

MESOGLŒA. A noncellular gelatinous layer in cœlenterates, lying between the ectoderm and the endoderm.

MESOZOIC. The Age of Reptiles. The geologic era between the Palæozoic and the Cenozoic.

METABOLISM. The sum total of the chemical processes that go on in the living body.

METAGENESIS. The alternate appearance of two forms in the same species, one of which reproduces sexually and the other asexually. See ALTERNATION OF GENERATIONS.

METAMERE. One of the series of homologous segments in metameric organisms.

METAMERISM. The process or condition of embryonic transverse fission resulting in the segmental structure seen in annelids, arthropods, and vertebrates.

METAMORPHOSIS. The transformation of a larva into an adult.

METAPHASE. The climax of mitosis involving the longitudinal splitting of the chromosomes.

METAZOA. A subkingdom of animals characterized by somatic specialization and unity of organization. Commonly, multicellular animals.

MICROGAMETE. The smaller of the two types of gametes in species exhibiting heterogamy.

MICROMERE. One of the quartet of smaller cells at the eight-cell stage of cleavage in the egg of the frog, etc., destined to form the ectoderm.

MICRONUCLEUS. The smaller of the two nuclei in Paramecium and its allies, supposed to function chiefly in reproduction. See MACRONUCLEUS.

MIMICRY. The resemblance of a defenseless species to a well-defended one, presumably as an adaptation for protection.

MIRACIDIUM. The earliest larval form of a trematode worm such as the liver fluke.

MITOCHONDRIA. Organized cytoplasmic bodies in animal cells.

MITOSIS. Cell division involving the formation of chromosomes and a spindle.

MOLECULES. The smallest particles into which any substance can be divided without changing their chemical character.

MOLLUSK. A member of the Phylum Mollusca.

MONŒCIOUS. Same as HERMAPHRODITIC.

MONOHYBRID. The progeny derived by mating two individuals differing in but one pair of alternative characters or genes.

MONOZYGOTIC. Referring to twins or larger numbers of offspring derived from a single fertilized egg or zygote. See DIZYGOTIC.

MORPHOLOGY. That branch of biology which deals with the form or structure of organisms.

MUTATION. Any heritable modification initiated in the germ plasm.

MYRMECOPHILOUS. Literally, ant-loving. Technically, commensal with ants.

NARES. Internal or external openings of the nasal passages.

NATURAL SELECTION. Charles Darwin's theory of Evolution, which has been paraphrased as "The Survival of the Fittest."

NAUPLIUS. The type of larva typical of the more primitive Crustacea.

NEMATOCYST. One of the stinging bodies characteristic of cœlenterates.

NEMATODE. A roundworm belonging to the Class Nematoda.

Neoteny. The retention of larval characters throughout life; becoming sexually mature while retaining larval characters.

Nephric Tubule. The structural unit of a vertebrate kidney. Similar to a Nephridium.

Nephridium. A tubular excretory organ, characteristic of many invertebrates.

Nephrostome. The funnel-like opening at the inner end of a nephridium.

Nerve. A group or bundle of nerve fibers.

Nerve Cell. A cell specialized for the transmission of excitation.

Nerve Fiber. A filamentous cytoplasmic extension of a nerve cell.

Nerve Impulse. A state of excitation transmitted along a nerve fiber.

Neural Groove, Tube. Same as Medullary Groove, Tube.

Neurilemma. The delicate external membrane covering a nerve fiber.

Neurone. A nerve cell, including the cell body and all of its processes.

Newt. A tailed amphibian.

Nitrifying Bacteria. Bacteria that oxidize ammonia to nitrites, and nitrites to nitrates.

Nitrogen-Fixing Bacteria. Bacteria which form nitrogen compounds from free nitrogen.

Nodes of Ranvier. Places in a nerve fiber where the medullary sheath is interrupted.

Nondisjunction. The failure to separate after synapsis on the part of homologous chromosomes, so that both of the latter go to one daughter cell and none to the other.

Notochord. Typically, a cylindrical rod of cells in chordates, lying ventral to the spinal cord and dorsal to the alimentary tract.

Nucleolus. The true nucleolus, as distinguished from the chromatin nucleus. The same as the Plasmosome.

Nucleoplasm. The protoplasm of which the cell nucleus is composed. In contrast with Cytoplasm.

Nucleus. A specialized protoplasmic body in most typical cells.

Nutrition. The intake of food substances, their distribution within the organism, metabolism, and elimination of waste products.

Occipital Condyle. A part of the base of the skull that serves as a pivot by means of which the head is articulated with the first vertebra.

Œsophagus. The passage leading from the pharynx to the stomach.

Olfactory. Pertaining to the sense of smell.

Ontogeny. The developmental history of the individual. See Phylogeny.

Oöcyte. A fully grown ovarian egg cell prior to the second maturation.

Oögenesis. The process of the development of the mature egg from the primordial germ cell.

OÖGONIUM. One of the early germ cells of a female prior to the beginning of the processes of maturation.

OÖTID. A mature egg. Comparable with SPERMATID.

OPERCULUM. A fold of skin covering the gills in the tadpole larva of the frog. Also, a plate used for closing the shell in gastropod mollusks.

OPTIC LOBES. Thickenings of the dorsal surface of the mid-brain.

OPTIC NERVES. The nerves connecting the eye with the brain.

ORAL. Pertaining to the mouth.

ORDER. A taxonomic group ranking below a class and above a family.

ORGAN. A complex of tissues subserving a specific function.

ORGANELLE. A specialized structure in a unicellular organism playing a rôle equivalent to that of an organ in a metazoan organism.

ORGANISM. A living individual, whether animal or plant.

ORGANISMAL THEORY. A doctrine that emphasizes the idea that the organism is a unit and that its unity consists in the centralized control of one dominant region over all subordinate regions. See ELEMENTAL THEORY.

ORTHOGENESIS. Definitely directed variation. The idea that repeated variations in the same direction occur in a race or a species, and that these changes are due to internal causes.

OSMOSIS. Diffusion of dissolved substance through a semi-permeable membrane.

OSMOTIC PRESSURE. The pressure exerted in a solution by the dissolved substance.

OSTIUM. A valvular opening through the wall of the heart in arthropods. Also the opening in a sponge through which it takes in water.

OVARY. The organ in which the germ cells of a female are formed or lodged.

OVIDUCT. A tube through which eggs leave the ovary.

OVIPARITY. The condition of being oviparous.

OVIPAROUS. Egg-laying. See VIVIPAROUS.

OVULATION. The process of giving off full-grown eggs from the ovary.

OVUM. An egg. A mature female gamete. Same as OÖTID.

OXIDATION. The chemical combination of any substance with oxygen.

OXYHÆMOGLOBIN. Hæmoglobin combined with a certain amount of oxygen.

PÆDOGENESIS. Precocious sexual maturity. Sexual maturity in an embryo or larva.

PALÆONTOLOGY. The science of ancient life. It deals with fossils of prehistoric organisms.

PALÆOZOIC. Pertaining to the geological era prior to the Mesozoic; commonly called the age of invertebrates and fishes.

PANCREAS. A gland, opening into the intestine, that secretes several important digestive enzymes.

PARAPODIUM. A flat, fleshy segmental projection characteristic of marine annelids, used for locomotion and respiration.

PARASITE. An organism that lives in or on another (the host) at the expense of the latter.

PARENCHYMA. A kind of loose, spongy mesodermal tissue found in some of the lower types of animals.

PARIETAL GANGLION. One of the ganglia characteristic of mollusks.

PARTHENOGENESIS. The development of an egg without fertilization.

PATHOLOGIC. The condition of being diseased.

PECTORAL GIRDLE. A group of bones or of cartilages serving to connect the fore limbs of vertebrates to the axial skeleton. See PELVIC GIRDLE

PECULIAR. When used to describe a species it means that such a species is not found anywhere else except in the place designated.

PEDAL DISK. The basal attachment disk of a Hydra.

PEDAL GANGLION. A ganglion associated with the activity of the foot in mollusks.

PEDICELLARIÆ. Minute automatic pincher-like structures characteristic of the surface of starfishes and sea urchins.

PELLICLE. A thin protective layer on the surface of a cell.

PELVIC GIRDLE. A group of bones connecting the fore limbs to the main skeleton.

PENIAL. Pertaining to the penis.

PENIS. The copulatory organ of many species of animals.

PEPSIN. The enzyme of the stomach that acts in the digestion of proteins.

PEPTONE. A substance derived by digestion (hydrolysis) of proteins.

PERICARDIUM. The peritoneum lining the pericardial cavity.

PERIOSTEUM. The living epithelial membrane on the outer surface of bone that functions as a producer of new bone cells.

PERIPHERAL NERVOUS SYSTEM. That part of the nervous system of a vertebrate that is made up of the spinal and cranial nerves.

PERISTOMIUM. The second segment in the body of an annelid worm; the segment into which the mouth opens.

PERITONEUM. The membrane lining the cœlom of vertebrates. This is continuous with the mesenteries.

PETRIFICATION. The process of substituting mineral matter for organic matter during the disintegration of an animal or plant. A method of fossilization.

PHARYNGEAL CLEFT. See GILL SLIT.

PHARYNX. That part of the digestive tract that belongs to the head; in invertebrates, that part of the digestive tract between the mouth and the œsophagus.

PHENOTYPIC. Pertaining to the somatic or expressed hereditary characters of an organism or group irrespective of their germinal constitution. See GENOTYPIC.

PHOTOSYNTHESIS. The formation of carbohydrates from carbon dioxide and water by the absorption of sunlight by chlorophyll.

PHOTOTAXIS. Response to light on the part of organisms.

PHYLOGENETIC. Pertaining to the ancestral history of a species or race.

PHYLOGENY. The ancestral history of the race. See ONTOGENY.

PHYLUM. One of the main taxonomic divisions of a kingdom or subkingdom.

PINEAL BODY. A small glandular structure on the dorsal side of the brain in vertebrates; believed to be a vestige of a third eye.

PITUITARY BODY. A glandular body beneath the brain, derived partly from the nervous system and partly from the alimentary tract.

PLACENTA. An embryonic structure characteristic of the higher mammals serving as an organ by means of which the mother imparts nourishment to the fetus.

PLACOID SCALE. The type of scale characteristic of the elasmobranch fishes.

PLASMA. The fluid part of the blood; blood from which all solid or semisolid ingredients have been removed.

PLASMAGEL. The relatively solid, or viscous, phase of protoplasmic colloids. Opposite of PLASMASOL.

PLASMA MEMBRANE. The surface membrane of the cytosome, composed of living protoplasm, and having the property of being semipermeable. To be distinguished from CELL WALL, which is outside of the cytosome and not a part of the latter. Same as CELL MEMBRANE.

PLASMASOL. The relatively fluid phase of protoplasmic colloids. In contrast with PLASMAGEL.

PLASMASOME. The true nucleolus. A formed component of the nucleus, not composed of chromatin. Of unknown function. To be distinguished from karyosomes, or chromatin nucleoli.

PLASTID. One type of formed component of the cytosome, fairly massive in form and functioning as a localized area of specific chemical transformation.

PLEURAL CAVITY. That part of the cœlom which contains the heart and lungs in mammals.

PLEURAL GANGLION. One of the characteristic ganglia of the mollusks.

PLEURO-PERITONEUM. A membrane lining the pleural cavity.

POLAR BODY. A small nonfunctional cell or gamete produced during the maturation divisions of the egg cell. An abortive oöcyte or oötid.

POLIAN VESICLE. A bulbous organ connected with the water-vascular ring in echinoderms.

Pollination. The transfer of pollen to the stigma of a plant.

Polyembryony. The production of two or more individuals from a single embryo or zygote.

Polymorphism. The occurrence of several types, or castes, of individuals in a colony or community of individuals belonging to the same species and derived from the same parent or parents.

Polyp. One of the hydra-like or feeding individuals in a hydroid or coral colony.

Posterior. Pertaining to that part or end of an organism opposite to the head.

Potential Energy. Energy inherent in the position or configuration of the component parts of a body or a chemical molecule.

Predaceous. Characterized by preying on other organisms.

Preformation. The doctrine that the adult organism is represented in miniature in the germ cell. See Epigenesis.

Pregnancy. The state of being with young.

Proboscis. A tubular extension of the nose or of the lips.

Proglottid. One of the individuals in the chain of zoöids produced by transverse fission in a tapeworm.

Prophase. That period of mitosis prior to the metaphase.

Prostomium. The first segment of the body in annelid worms; the segment anterior to the mouth.

Proteid. Pertaining to proteins. Same as Protein.

Protein. A class of complex chemical substances containing nitrogen, making up an essential part of protoplasm.

Proteose. Any one of a number of substances derived from the hydrolysis of proteins.

Protista. A group consisting of both unicellular animals and plants.

Proton. A particle of positive electricity, one of the ultimate constituents of all matter. See Electron.

Protoplasm. The physical basis of life; the living matter of which organisms are composed.

Protopodite. The basal segment of the typical biramous appendages of the crayfish and its allies.

Prototroch. The equatorial band of cilia in the Trochophore larva.

Protozoa. A subkingdom (phylum) of animals characterized by being unicellular.

Protozoölogy. That branch of animal biology that deals especially with Protozoa.

Proventriculus. The first division of the stomach in the birds.

Pseudopodia. The blunt fingerlike projections used by Amœba and its relatives for locomotor or feeding activities.

PULMONARY. Pertaining to the lungs.

PUPA. A quiescent stage in the development of insects, between the larval and adult stages.

PURE LINE. A group of individuals possessing identical genes and derived from a homozygous ancestor.

PYLORIC VALVE. A muscular constriction between the stomach and the small intestine.

QUADRATE. One of the bones of the skull in some vertebrates.

QUADRUPLET. One of a set of four offspring derived from a single zygote. In human beings, one of four individuals born together from the same mother.

RADIAL CANALS. The water-vascular canals radiating from the water-vascular ring in echinoderms.

RADIAL SYMMETRY. The arrangement of the principal parts of an organism like the spokes of a wheel.

RADIANT ENERGY. Energy transmitted through "empty space"; including light, X-rays, etc.

RADIO-ULNA. The fused radius and ulna bones of the frog.

RADIUS. The bones of the fore-arm located on the thumb side of the limb.

RADULA. A ribbonlike rasping organ used for purposes of mastication in certain mollusks.

RECAPITULATION, LAW OF. The doctrine that the life history of the individual is equivalent to a much abbreviated résumé of the ancestral history of the race.

RECESSIVE. Referring to a gene that does not express itself in the soma in the presence of a contrasting dominant gene.

RECTUM. The terminal portion of the large intestine.

REDIA. An individual belonging to the second type of larva found in the life history of the liver flukes and their kin.

REDUCTION. The cell divisions in the germ cell cycle in which chromosomes, at one division, do not split lengthwise, but merely separate after associating for some time in pairs. Refers to a numerical reduction of chromosomes to one half that typical for the soma.

REFLEX ACTION. An action performed as the result of an impulse that travels over a reflex arc. It is involuntary and may be quite unconscious.

REFLEX ARC. A series of neurones transmitting excitation successively from a receptor through the central nervous system to an effector.

REGENERATION. The process of, or power of, replacing a lost part; the development of a whole individual out of a part.

RENAL. Referring to the kidneys.

REPRODUCTION. The process of producing, or power of organisms to produce, offspring.

Reptile. A member of the vertebrate Class Reptilia.

Reservoir. A large water vacuole into which empty the numerous small contractile vacuoles, as in Euglena and other flagellate Protozoa.

Respiration. The process of obtaining energy from food, involving at least some phases of oxidation.

Resting Cell. One which is not undergoing mitosis.

Reticular Theory. A theory of the ultimate structure of protoplasm, according to which all structures are composed of networks of fibrils.

Retina. The actual sensory part of the eye, composed of layers of light-sensitive cells.

Rhabdites. Rodlike bodies in the epidermis of flatworms whose function is not fully understood.

Rheotropism. The reaction of organisms to currents.

Rotifer. Any one of the small aquatic animals belonging to the Phylum Trochelminthes.

Rugose. Ridged or furrowed.

Salamander. One of the tailed Amphibia belonging to the Order Urodela.

Saliva. The fluid secreted by the Salivary Glands.

Salivary Glands. Glands emptying into the mouth of an animal, which secrete saliva, a digestive juice that starts the processes of digestion.

Salt. A substance which produces positive ions other than H^+ and negative ions other than OH^-.

Saprophytic. Obtaining organic food substances by absorption from the dead remains of organisms or their products.

Sarcode. The term first applied to protoplasm, by Dujardin.

Sarcolemma. The delicate membrane surrounding a voluntary muscle cell.

Sarcomere. One of the apparent segments into which each muscle fibril is transversely subdivided.

Sarcoplasm. The protoplasm of a striated muscle cell.

Scolex. The head, or attaching individual, in the linear series of individuals making up a tapeworm.

Secondary Sexual Characters. Morphological, physiological, or behavioral differences between the sexes other than those involved in the gonads, or primary sex organs.

Secretin. A hormone, produced by the epithelial cells lining the intestine, which stimulates the pancreas and liver to secrete their appropriate juices.

Secretion. The elimination from cells of substances which have been synthesized or accumulated in these cells. Any substance or mixture thus secreted.

Sedentary. Referring to organisms with sluggish habits that move about only to a minimal extent.

SEGMENTATION. Same as METAMERISM. Sometimes used as a synonym for CLEAVAGE.

SEGMENTATION CAVITY. The hollow of the blastula. Same as BLASTOCŒLE.

SEGREGATION. The separation of contrasting genes into different gametes.

SEMICIRCULAR CANALS. That part of the vertebrate ear devoted to the sense of equilibrium.

SEMINAL RECEPTACLES. Saclike bodies within the body of the earthworm which receive sperms from another worm and hold them until the eggs are ready for fertilization.

SEMINAL VESICLES. Large reservoirs associated with the testes in the earthworm whose function is to harbor the sperms during most of the period of spermatogenesis.

SEMIPERMEABLE. Permitting the passage of solvents but being relatively or entirely impermeable to dissolved substances.

SENSE ORGAN. A multiple receptor organ, including sensory cells and accessory structures associated with them.

SENSORY. Pertaining to sensation. Applied to a nerve cell which transmits an impulse resulting in a sensation.

SENSORY CELL. A unicellular receptor.

SENSORY NEURONE. A neurone which either acts as a receptor itself or receives excitation directly from a receptor which is not a neurone: its axone usually runs into the central nervous system.

SEPTA. The partitions that divide the cœlom of the earthworm into metameric chambers. See DISSEPIMENT.

SERIAL HOMOLOGY. The homology of one metameric structure to another in a different metamere; e.g., the various appendages of the crayfish are serially homologous.

SERTOLI CELLS. Modified testicular cells that seem to act as nurse cells for immature spermatozoa.

SERUM. The clear fluid of the blood that is left after the blood has clotted and the clot is removed. It contains many specific materials in solution.

SESSILE. Attached directly, as distinguished from stalked. More commonly, attached, as opposed to free-living.

SETÆ. Same as CHÆTÆ.

SEX CHROMOSOME. The odd or X-chromosome whose presence or absence determines whether a gamete shall be male-producing or female-producing.

SILICIOUS. Composed of silica (Silicon dioxide).

SINUS VENOSUS. A large thin-walled blood chamber on the dorsal side of the heart into which empty the main trunk veins and which, in turn, opens into the right auricle through the sinu-auricular valve.

SIPHON. A passageway for currents of water; as the openings between the right and left mantle of clams and mussels, where the edges do not meet.

SOLAR SYSTEM. A star-sun with all its planets, etc.

SOLUTE. A substance dissolved in another.

SOLVENT. A substance in which another is dissolved.

SOMA. The body of an organism, contrasted with the germ cells.

SOMATIC. Pertaining to the body, or soma.

SOMATOGENIC REPRODUCTION. That type of reproduction that is effected by a division of a multicellular body, or soma, by means of fission, budding, etc. In contrast with CYTOGENIC REPRODUCTION.

SOMITE. One of the segments or metameres of a metameric organism such as the earthworm.

SPECIAL CREATION. The doctrine that each of the species as we know them today was specially created.

SPECIALIZATION. Structural or functional emphasis upon one or a few functions.

SPECIES. A group of individuals so nearly alike that they might have been derived from the same parents. In classification, the main subdivision of a genus.

SPERM. Same as SPERMATOZOÖN. A male gamete.

SPERMARY. Same as TESTIS.

SPERMATID. A male germ cell after the second maturation but before becoming specialized to form the typical spermatozoön.

SPERMATOCYTE. A male germ cell resulting from the last generation of spermatogonia; also male germ cells after the first maturation division.

SPERMATOGONIUM. An early male germ cell prior to the onset of changes leading to maturation.

SPERMATOZOÖN. The definitive male gamete in animals. See SPERM.

SPICULE. A needle-like skeletal structure seen in sponges.

SPINAL COLUMN. The series of vertebræ in vertebrates.

SPINAL CORD. That part of the central nervous system of vertebrates posterior to the brain and largely inclosed in the neural canal of the vertebræ.

SPINDLE. The assemblage of threads or fibers that are associated with the chromosomes in mitosis and that assume a more or less spindle-like form.

SPINDLE CELL. One type of cell characteristic of frog's blood.

SPIRACLE. In frog tadpoles, the opening on the left side through which water passes from the gill chamber to the outside.

SPIREME. The coiled thread or threads of chromatin seen during the prophases of cell division.

SPLEEN. A vascular organ characteristic of most vertebrates. Lies near the stomach and has a function connected with the breakdown of worn out red blood corpuscles and with the destruction through phagocytosis of invading bacteria.

SPONGIN. A horny material forming the skeleton of bath sponges.

SPONTANEOUS GENERATION. Same as ABIOGENESIS.

SPORE. A reproductive cell liberated from a parent, capable of giving rise without fertilization to a new individual. A reproductive cell which is not a gamete.

SPOROCYST. A saclike individual formed from the miracidium of a liver fluke.

SPOROZOITE. A stage in the life cycle of the malaria organism (and allied forms) before it enters the red blood cell of man.

SPORULATION. The process of forming spores.

SQUAMOUS. Scaly. Referring to a kind of epithelium composed of flat scalelike cells.

SQUID. An animal belonging to the Class Cephalopoda, Phylum Mollusca.

STARCH. A complex carbohydrate. The chief stored food substance of green plants.

STATOBLAST. A group of cells constituting the asexual reproductive unit of the Bryozoa. A sort of internal bud.

STEAPSIN. An enzyme secreted by the pancreas, which hydrolyzes fats and some other lipins.

STIMULUS. Any condition which calls forth a response in living matter.

STOMODÆUM. That part of the lining of the mouth which is formed by an inturning of the ectoderm.

STRATIFIED. Arranged in strata or layers.

STRIATED. Cross-striped or cross-banded. Referring to one of the principal types of muscle fibers. See UNSTRIATED.

SUPRARENAL GLAND. A ductless gland in vertebrates that lies above the kidney. Same as ADRENAL GLAND.

SURFACE TENSION. A term describing the fact that the surface layer of fluids is under a tension. This results in the tendency of small masses of fluid to reduce the surface to a minimum and thus to assume the form of spherical droplets or vacuoles.

SUSPENSION. A dispersion consisting of solid particles in a liquid medium.

SWIMMERET. A primitive biramous appendage beneath the abdomen of crayfish.

SYMBIOSIS. The living together of two species supposedly for mutual benefit.

SYMPATHETIC NERVOUS SYSTEM. A system of ganglia and nerves that are associated with the viscera and which communicates with the central nervous system by way of the roots of the spinal and cranial nerves.

SYNAPSE. A point of contact between two neurones.

SYNAPSIS. The pairing and lying in contact of homologous chromosomes prior to maturation of the germ cells.

SYNCYTIAL. Pertaining to a SYNCYTIUM.

SYNCYTIUM. An undivided mass of protoplasm containing many nuclei.

SYNGAMY. The union of gametes to form a zygote.

TADPOLE. The larva of a frog.

TAPEWORM. A member of the Class Cestoda, Phylum Platyhelminthes.

TAXONOMY. The science of classification.

TELOPHASE. The final phase of mitosis, during which daughter nuclei are reconstructed.

TERMITES. Social insects belonging to the Order Isoptera; commonly called "white ants."

TEST. The hard outer shell of the sea urchin or other animals.

TESTIS. The male gonad. The organ in which male germ cells are formed or are lodged. See SPERMARY.

TETRAD. A quadruple chromosomal body composed of paired homologous chromosomes each of which has precociously divided.

THALAMENCEPHALON. A part of the vertebrate brain derived from the primitive fore-brain.

THERMOTROPISM. The response of organisms to changes of temperature.

THIGMOTROPISM. The response of organisms to mechanical contacts.

THROMBIN. A specific material, probably an enzyme, that causes clotting of the blood.

THYROID EXTRACT. An extract of the active principle of the thyroid gland, whose essential constituent is iodine.

THYROID GLAND. An endocrine gland in the neck region of vertebrates that has the function of regulating the rate of growth, metabolism, etc., of the whole organism. An extremely important chemical regulatory mechanism.

THYROXIN. A hormone secreted by the thyroid gland.

TISSUE. A group of cells of similar structure and function making up a continuous mass or layer.

TRACHEÆ. Tubes carrying air to and from the lungs in vertebrates. Also air tubes used for respiration in various arthropods.

TRIAL AND ERROR. The name applied to the theory that organisms find their way to favorable regions by continually avoiding less favorable regions. In contrast with the TROPISM THEORY.

TRICHOCYSTS. Minute rodlike bodies lying in the cortex of Paramecium, and other Infusoria, that are supposed to play a protective rôle.

TRIHYBRID. The offspring of parents differing with regard to three alternative genes or characters.

TRILOBITE. A kind of extinct arthropod.

TRIPLOBLASTIC. Having the three primary germ layers: ectoderm, endoderm, and mesoderm. See DIPLOBLASTIC.

TROCHOPHORE. A nearly spherical type of ciliated aquatic larva characteristic of flatworms, annelids, mollusks, etc.

TROPISM. A response of an organism to a particular stimulus. Referring to a theory of animal behavior sometimes known as the "machine theory." See TRIAL AND ERROR.

TRYPANOSOME. A parasitic protozoan belonging to the Class (Phylum) Mastigophora. The biological basis of sleeping sickness.

TRYPSIN. A ferment produced by the pancreas which has the power of digesting proteins.

TSETSE FLY. A species of fly which carries the germs of sleeping sickness.

TUBE-FEET. Tubular locomotor organs characteristic of echinoderms.

TUNICATE. A member of the Class Ascidiacea, Phylum Chordata.

TWINNING. The process of symmetrical longitudinal fission of a cell or of an organism resulting in the production of two equivalent individuals, or twins.

TYMPANIC MEMBRANE. Same as eardrum.

TYPHLOSOLE. A median dorsal invagination along the whole length of the intestine of the earthworm, whose rôle seems to be that of increasing the digestive surface.

UNIT CHARACTER. A character inherited more or less like a unit and independently of other characters.

UNIVERSAL SYMMETRY. A type of symmetry in which all radii from the center to the surface of an organism are approximately equal.

UREA. A simple organic compound, $CO(NH_2)_2$, the chief nitrogenous waste product of most animals. Contains considerable potential energy.

URETER. The duct carrying urine from the kidney to the cloaca or to the surface of the body.

URINE. The secretion of the kidneys.

UROGENITAL SYSTEM. A complex system of organs in vertebrates concerned with both excretion and reproduction.

UTERUS. The lower, usually enlarged, portion of the oviduct in which incubation of eggs takes place; in mammals, the womb.

VACUOLE. A region within a cell occupied by fluid other than protoplasm.

VAGINA. The passage leading from the uterus to the exterior.

VALVE. A flap or pocket in the heart or main arteries of vertebrates or other animals whose function it is to prevent back flow of the blood. An entirely different use of the term is that in connection with the shells of bivalve mollusks; each of the two shells is called a valve.

VASCULAR. Pertaining to blood vessels or blood supply.

VAS DEFERENS. A duct conveying sperms from the testis to the exterior.

VEGETAL POLE. The pole of the egg where the rate of metabolism is lowest. That pole opposite to the ANIMAL POLE.

VENTRAL. Literally, pertaining to the belly. Referring to the lower side.

VENTRICLE. The muscular pumping part of the heart of vertebrates and other animals.

VERTEBRÆ. The series of short bones making up the spinal column, or backbone.

VERTEBRAL COLUMN. See SPINAL COLUMN.

VERTEBRATE. An animal possessing a spinal column, or backbone.

VESTIGIAL. Rudimentary, or reduced to a mere vestige of a one-time size or functional importance.

VISCERA. Internal organs of animals.

VISCERAL MASS. One of the chief subdivisions of a mollusk, containing the chief organs of nutrition, excretion, circulation, and reproduction.

VISCERAL SKELETON. That part of the skeleton of the vertebrates consisting of the bones of the jaws, of the tongue, and of the branchial arches.

VISCOSITY. Quality or state of being viscous, or imperfectly fluid, a quality characteristic of protoplasmic colloids that are more or less in the plasmagel state. A characteristic feature of a viscous material is that it flows relatively slowly.

VITALISM. The doctrine that attributes at least some of the phenomena of life to the interplay of forces different from those which prevail in the lifeless world. See MECHANISTIC VIEW.

VITAMINES. Substances of unknown chemical constitution, but essential for the maintenance of life and of health.

VITELLINE GLAND. An organ producing yolk to be supplied to growing eggs.

VITELLINE MEMBRANE. A membrane surrounding an egg.

VIVIPAROUS. Producing young from eggs that are retained in the uterus until they are hatched and able to move about of their own accord. In some animals the young are nourished in the uterus up to an advanced stage through a nutritive communication between the maternal and fetal tissues.

VOMER. One of the bones of the under side of the vertebrate skull.

VOMERINE. Related to, or upon, the vomer.

X-CHROMOSOME. The peculiar chromosome in a germ cell that determines the sex of the zygote.

Y-CHROMOSOME. A peculiar chromosome often the partner of the X-chromosome and having to do with the fertility of males.

ZOÖGEOGRAPHY. That branch of zoölogy that deals with the geographic distribution of animals.

Zoöid. An individual belonging to a colony such as that of hydroids. A term also used for subordinate individuals formed by transverse fission in Planaria and its relatives.

Zygote. A fertilized egg. A cell produced by the union of gametes.

Zygotic. Pertaining to a zygote.